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The role of ontogenetic habitat shifts on the parasite communities of five South Florida fishes

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Thesis of
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Submitted in Partial Fulfillment of the Requirements for the Degree of

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HALMOS COLLEGE OF NATURAL SCIENCES AND OCEANOGRAPHY

The role of ontogenetic habitat shift on parasite communities in five South Florida fishes

By

Brittany Nicole White

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Halmos College of Natural Sciences and Oceanography
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Abstract

Many reef fishes initially recruit into mangroves, and then migrate out to reef habitats as they grow and mature. Each ontogenetic habitat shift exposes migrants to previously unencountered parasite taxa, potentially increasing parasite species richness and driving changes in parasite community structure. However, studies on this topic rarely attempt to distinguish between the location effects of habitat shifts versus a simple increase in physical size. Therefore we contrasted parasite community richness and structure in Great Barracuda *Sphyraena barracuda* (N=84), Atlantic Needlefish *Strongylura marina* (N=49), Crevalle Jack *Caranx hippos* (N=59), White Mullet *Mugil curema* (N=90), and Yellow-fin Mojarra *Gerres cinnerus* (N=60) from three locations: mangrove, inshore seagrass beds, and offshore reef habitats. Mullet harbored the highest species richness (S=26, mean infracommunity S=2.4±1.6) and Atlantic Needlefish the lowest (S=8, mean infracommunity S=0.5±0.8). A global model including species, location, and size class was significant (R^2=0.654, DF 17, F=35.91, p<0.001), with location (LogWorth 6.0) and size class (LogWorth 4.9) having the strongest effect; furthermore there was a significant species by location interaction (p<0.001, LogWorth 14.6). PERMANOVA on Bray-Curtis similarities found that both location and size significantly structured parasite communities for all species, with habitat shift (pseudo-F 3.3) having a larger effect than size (pseudo-F 1.8). As with species richness, there was a significant location by species interaction (pseudo-F 4.6). Ordination analyses indicated that parasite community structure was similar among species during their juvenile mangrove stage, but changed significantly as individuals initiated shifts to seagrass beds; community structural changes associated with the final shift to reef habitats were less pronounced in all taxa except White Mullet. Our results suggest that ontogenetic habitat shifts and (to a lesser extent) host size class are important drivers of parasite community composition and structure in these fishes.

Keywords: Parasites; Reef Fishes; Community Ecology

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Introduction

Many adult reef-associated fishes initially recruit into estuarine and mangrove environments, then subsequently migrate into reef habitats as they grow and mature. This semi-permanent migration or ontogenetic habitat shift requires transit through various coastal habitats, each with characteristic prey communities and trophic interactions. These movements are known to be driven to some extent by food availability, climate and habitat features, and predator avoidance (Altizier et al. 2011); migrating fish integrate information from environmental ads navigation cues with their own energy budget and resource use. For an individual fish to shift habitats, the benefits must significantly outweigh the fitness and physiological costs, as well as the inherent risks, including increased risk of injury and predation (Altizier et al. 2011). Given the inherent energetic cost and danger, ontogenetic habitat shifts must therefore confer evolutionarily significant benefits.

Although the effect of host growth, age, and (to a lesser extent) ontogenetic diet shifts on parasite communities have been addressed in several studies (e.g., O'Dwyer et al. 2014), few have explicitly addressed the role of changing habitats, and fewer still have involved fish hosts (e.g., Henriquez et al. 2011). We hypothesize that these individuals are undergoing ontogenetic habitat shift to escape the areas where parasite prevalence is high. This hypothesis is supported by Poulin et al. (2012) and Alitzer et al. (2011), who interpret ontogenetic niche shifts as a form of migratory escape. Migratory escape occurs when infectious stages of parasites build up in an environment such as an estuary or mangrove habitat and cause potential host species to migrate out of that habitat in order to avoid infection. For example, many species are known to shift habitats to avoid accumulating parasites in any given locality, which might lead to high rates of life-history stage-specific mortality (Altizer et al. 2011). Migratory escape scenarios predict that parasitism would be generally low in both juveniles and migrants. Parasitism may drive migratory patterns in other ways, for instance by preventing heavily infected juveniles from initiating ontogenetic habitat shift; under this paradigm, heavily infected fish are unable to migrate, so migrant populations that successfully complete ontogenetic habitat shifts would harbor fewer parasites than non-migrating conspecifics (Welicki and Sikkel

2015). This study will address these competing hypotheses in local fishes.

Parasites in the inshore reef environments are the most highly diverse of all of the ocean habitats (Marcogliese 2002). The five fishes studied here alone have been previously found to be infected with over 54 different parasite families (see Appendix 1 for complete list of reported parasites in these fish species). The sub-tropical mangrove and reef tracts are highly diverse with a large variety of flora and fauna as well as a highly productive stable environment (Marcogliese 2001). Parasites in the marine system tend to be generalists at the levels of both intermediate host and definitive host, and are also usually long-lived, allowing them to indiscriminately infect hosts and be transferred to new hosts, even in a dilute environment (Marcogliese 2002). The high species diversity in the marine ecosystem and the low specificity for intermediate hosts allow for a higher number of transmission pathways and potential opportunities for infection in these environments (Marcogliese 2001). The gregarious nature of reef fishes and invertebrates as well as the migration behavior of many of these organisms effectively favors transmission into new hosts (Marcogliese 2002). Although most inshore parasites are generalists, it is not uncommon to for fish hosts to have distinctly different parasites communities within the same ecosystem (Marcogliese 2002).

The five host fish species considered here are Great Barracuda *Sphyraena barracuda*, Atlantic Needlefish *Strongylura marina*, Crevalle Jack *Caranx hippos*, White Mullet *Mugil curema*, and Yellowfin Mojarra *Gerres cinnerus*. All five species were selected for this study because they undergo ontongenetic habitat shifts throughout their lifetimes. All five of these species make use of mangrove and estuary habitats as initial nursery habitat until they are large enough to transition out to the reef habitats as adults (Figure 1). These species were also chosen because they are easily accessible and in high abundance in all three of the habitats studied in the surrounding South Florida area. These locations are (1) mangroves, (2) inshore seagrass beds, (3) reef habitats. Individuals of these five species cover most of the middle to high trophic levels within the ecosystem; and they also inhabit different levels within the water column which allows for a variety of benthic-surface interactions as well. Both trophic interactions as well as physical location within the water column are important for the host-parasite interactions within the ecosystems (Altizer et al. 2011).

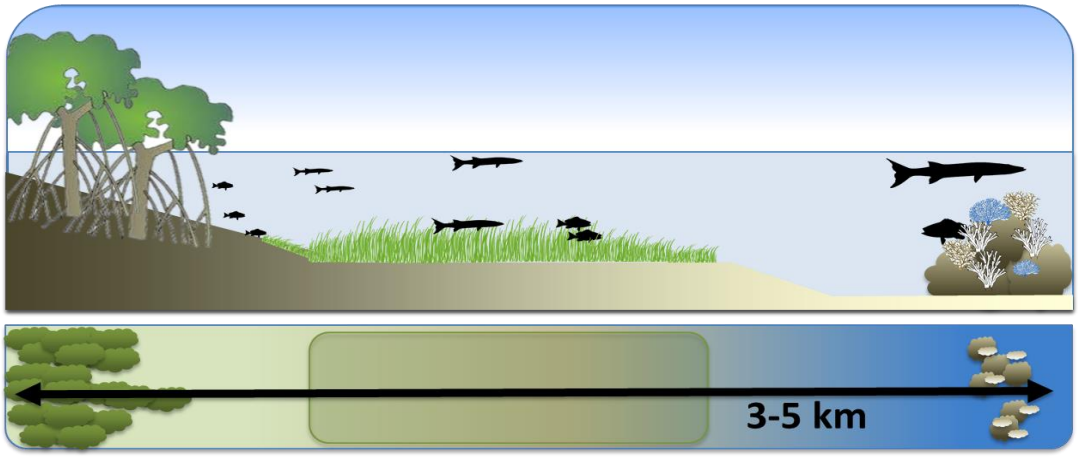

Figure 1. Conceptual diagram of the study ecosystem, showing the movement of fishes throughout this study mangrove → seagrass flat → reef continuum of Southeast Florida. Fish and other items within image are not to scale.

Marine intercoastal habitats are home to many different species of flora and fauna, including many that serve as both intermediate and definitive hosts for contagious and trophically-acquired parasites, including an abundance of juvenile reef fishes and multiple species of molluscs and arthropods (Nagelkerken et al. 2000). Reefs are among the most diverse ecosystems in the world (Grutter et al. 2003). The high diversity of potential hosts provides an increased chance for parasite transmission (Poulin 1995). Limited size-dependent space and high levels of competition for that space within the structurally complex mangrove prop root habitats and well as coral reef habitats lead to large aggregations of fishes and increased interactions between individuals causing an even larger change of parasite transmission from an infected fish (Nagelkerken et al. 2002). This was further validated by Graham & Nash (2013) who found a positive correlation between structural complexity and diversity, abundance and biomass of organisms within the inshore reef environments. The mangrove habitats tend to be high stress environments due to high amounts of sediment siltation and ersosion as well as variable salinity and nutrients due to tidal influences and runoff (Lugo 1980). The large environment variation in the mangroves makes transfer of contagious parasites (i.e., monogenea and digenea metacercariae) less efficient.Their free-living infectious stages are less likely more able to find new hosts within these variable environments without exerting large amounts of energy or experiencing high levels of mortality (Munoz and Zamara 2011).

The majority parasite families that are found in the marine environment are trophically acquired. These parasite families include Digenea, Nematoda, Acanthocephala, and Cestoda and will be collectively considered helminths. Many of the helminth parasites in the marine ecosystem rely on the ingestion of infected intermediate hosts in order to continue their life cycles (Lagrue et al. 2011). Therefore it is suggested that trophically acquired parasite infections are directly related to the diet preference of the host fishes. The diet of the five host fishes studied varies greatly by species and each of the fishes shows varying degrees of ontogentic diet shift that accompanies their movements from the mangrove habitats to the reefs (Table 1).

Table 1. Ontogenetic diet shift data for all studied fish species. Standard length measures in centimeters shows ranges of sizes in centimeters from fish sampled from each location. All references for size data denoted in superscript. [1](Porter & Motta 2004), [2](Abaraca-Arenas 2014), [3](Arceo-Carranza et al. 2014), [4](Zahorcsak et al. 2000), [5](Kwei 1978)

	Mangrove		Seagrass Beds		Reef	
	Size	Diet	Size	Diet	Size	Diet
S. barracuda[1]	11 – 30	Small Teleosts & Invertebrates	31 – 47	Small & Large Teleosts	48 – 111	Large Teleosts
M. curema[2]	3 – 17	Detritus & Plant Material	10 – 25	Plant Material & Protozoa	10 – 13	Plant Material & Protozoa
S. marina[3]	5 – 29	Invertebrates	29 – 43	Invertebrates & Small Teleosts	43 – 72	Invertebrates & Small Teleosts
G. cinereus[4]	2 – 10	Zooplankton	17 – 21	Benthic Invertebrates	15 – 22	Benthic Invertebrates
C. hippos[5]	5 – 10	Small Teleosts & Invertebrates	16 – 35	Small Teleosts	22 – 66	Large Teleosts

Purpose and Objectives

The overall premise of this study was to assess the changes in the parasite community composition and structure in five fish host species that undergo ontogenetic habitat shifts. The specific objectives were 1) to identify the ectoparasitic and endoparasitic communities to determine the overall observed species richness of all five common South Florida fishes in their three crucial life stages (juvenile, sub-adult, and adult); 2) determine how the parasite communities of these fishes change in composition and structure as they shift from mangrove habitats as juveniles to coral reef habitats as adults; and 3) explore the specific role of habitat in driving those changes and distinguishing that role from that played by age, size, and diet.

Materials and Methods:

Sample Collection

Samples were collected from three major habitats within the South Florida coastal ecosystem: mangroves, inshore seagrass habitats (represented by the Intercoastal Waterway (ICW)), and reefs from April 2014 – July 2017.The primary source of samples for the mangrove habitats came from Whiskey Creek, located within Dr. Von D. Mitzell-Eula Johnson State Park in Dania Beach, FL. Samples of the transient populations were collected in the ICW from Port Everglades, FL to Hallandale Beach, FL using. Reef population samples were collected off the reefs from Dania Beach, FL to Key Largo, FL. All fishes from the reef environment were caught on the first, second, and third reef tracts to ensure that an accurate subset of the population was sampled. The same sampling methods were used at all locations, with the exception of spearfishing in the mangroves, to ensure that complete size range for each location was sampled. The sampling methods included seine netting, cast netting, hook-and-line fishing, and spearfishing. All fishes were transported to the laboratory and either processed immediately, or individually bagged and frozen at -20 °C prior to examination.

Laboratory Pre-processing

Prior to processing, large (>30 cm total length (TL)) frozen specimens were placed in a lab refrigerator and allowed to thaw slowly. Small (<30 cm TL) frozen individuals were placed in a sealed plastic bag and thawed in a bucket of room temperature water or left out on laboratory bench until completely thawed. Fresh or refrigerated specimens were processed immediately. During processing, each fish was assigned a unique identification number and standard biometric measurements were recorded. The weight of the whole specimen was determined by a table top scale (Oharus Scout SKX621) for small specimens and a hanging scale for large specimens (PESOLA PHS100).

Laboratory Processing

The external surfaces of the individual were thoroughly examined for ectoparasites with a stereomicroscope. If the sample was bagged prior to processing, the inside of the bag was also examined for external parasites that may have fallen off during the freezing/thawing process. All fin rays and gill filaments/arches were removed from the body and examined individually by running tap water lightly over them and gently brushing with tweezers per Al-Zubaidy (2013), which dislodges any parasites attached to the sample without damaging them. The buccal cavity was then examined for additional ectoparasites and food particles. The eyes were removed from their sockets, dissected, and examined to determine if parasites were present in the humor, retina, or lens. All external parasites found in these organs were removed from the sample and placed into a small Petri dish filled with tap water to be counted. Counts were recorded and subsets of all parasites found were then either fixed in 95% ethanol or fixed in 70% ethanol (Arceo-Carranza 2004) prior to staining and mounting on slides for identification (Pritchard & Kruse 1982).

The body cavity was opened ventrally and the sex of the fish, if mature, was determined. All the internal organs (heart, liver, spleen, esophagus, pyloric caeca, stomach, spleen, gall bladder, intestines, gonads, kidneys, and swim bladder) were removed and placed in petri dishes to be examined for parasites under a stereomicroscope

(Fajer-Avila et al. 2006). Stomach and intestines from each individual fish were separated and opened to remove any unattached endoparasites, using a stir-rinse-repeat cycle in 100 mL glass jars filled with tap water. After the stir-rinse cycle was completed, the stomach and intestines were removed and pressed between two glass plates and viewed under the stereomicroscope to identify any attached parasites that were not removed by the initial process. The remaining fluid from the stir-rinse cycle was then left to settle. Once settled, the top layer of liquid and suspended material was decanted off of the sample. This process was repeated until the clarity of the sample was clear enough to identify any parasites left in the precipitate via a stereomicroscope. The empty body cavity was examined for endoparasites as well. Internal organs were compressed between two glass plates to more effectively examine them for parasites. The esophagus, pyloric caecae, liver, spleen, gall bladder, and gonads (if developed) were cut open ventrally and sectioned if needed and then compressed between the glass plates to be able to identify any parasites (Fajer-Avila et al. 2006). Identified parasites were dislodged from the organ with tap water and tweezers and placed in a small Petri dishes filled with tap water. A transverse incision posterior to the cranium was made to remove the brain and otoliths. The brain was compressed between two glass plates and examined for endoparasites similarly to the other bodily organs. Pectoral muscle sample were removed from directly behind the pectoral fin to identify any encysted parasites. The skin was removed from the sample and the muscle was pressed in between two glass plates and examined under a stereomicroscope. Incisions were made at the based on the dorsal and anal fins to determine whether subcutaneous nematodes were present.

All helminth parasites (monogeneans, digeneans, cestodes, and acanthocephalans) were removed from the host fish, counted, and fixed in 70% ethanol prior to staining and mounting. Once parasites were fixed, they were stained with acetocarmine (Pritchard & Kruse 1982), using a stain of 1 part acetocarmine to 3 parts 70% ethanol. The helminths were then dehydrated through a series of 70%, 95%, and 100% ethanol solutions (Moravec & Bakenhaster 2012) before being placed in clove oil to clear the internal body tissues. Helminths were permanently mounted on a glass microscope slide with Permount or Eukit (Fisher Scientific).

Nematodes were immersed in hot 70% ethanol to ensure that they fixed in an extended position. The nematodes were then placed in a 70% ethanol and 30% glycerol solution for a minimum of 14 days, and the ethanol slowly allowed to evaporate. Nematode specimens were examined and identified to lowest taxa via temporary wet mounts or in semi-permanent mounts of glyerine (Pritchard & Kruse 1982). All arthropod ectoparasites were examined and identified whole before being preserved unstained in 70% ethanol solution (Skinner 1978).

Species Identification

Final identification of all parasites was based on standard synthetic keys (Coull 1977; Hendrix 1994; Amin 1998; Dudley & Illg 1991; Anderson et al. 2009; Gibson 2010; Schell 1984; Gibson et al. 2005; Gibson 1996; Jones et al. 2002; Bray et al. 2008, Gibson 1996) and primary literature with indication of key species-specific structures and stages. Appendix 2 contains the full list of dichotomous keys, original and updated species descriptions, and primary literature used for species identification. The World Register of Marine Species (WoRMS) was used to synonymize all species in the literature with currently valid names. Scientific names that were *in sedis* or unaccepted without renaming were noted accordingly.

Data Analysis

The use of both univariate and multivariate analyses were used to examine the three objectives. Univariate analysis began with the calculation of mean parasite abundance at each lide stage, intensity and prevalence, as well as overall parasite species richness (Table 2). These measures were calculated in Microsoft Excel 2010 for each parasite and fish species. In the context of this study, *abundance* is the number of parasites of a given taxon that are found across all hosts, including both the infected and uninfected, *intensity* is the number of individuals of a particular taxon in a single infected host, *prevalence* is the number of hosts infected with one or more of a particular parasite taxon, and *overall species richness* refers to the number of parasite species found within each individual fish (Bush et al. 1997).

All studied fishes grow independently of one another at different rates so to determine the effect of individual size, each fish species was divided into four comparable size classes. These classes were determined on an individual species basis in PRIMER (v. 7.0.13; PRIMER-e (Quest Research Limited)) by using initially transforming the data by Log(X=1) and running resemblance between samples. The use of k means clustering along with a non-Metric MDS was used to determine the four size class clusters for each species. See Appendix 2 for size class clustering for each species. Each individual fish was assigned an appropriate size class that was used for the remainder of the data analyses.

For all multivariate diversity and community-level analyses, PRIMER 7.0.13 was used to generate parasite alpha and beta diversity indices, with special emphasis on measures of parasite species richness, total number of parasite species present, and equitability, how evenly the individual parasites are distributed among the host species (Clarke et al. 2014). These included calculating infracommunity and component community richness, as well as community evenness using and the Shannon index, which determines the proportion of total abundance arising from a particular species, and Hill numbers indices, which combines multiple indices including transformed Shannon diversity, the inverse of Simpson index and Reciporcal of Berger-Parker index (Magurran 2004). The *component community* refers to all the infracommunities of parasites associated with a subset of the host species. The *infracommunity* refers to the community of parasite infrapopulations within a single host (Bush et al. 1997). All parasite communities were considered to be nested within host species and all data analysis were structured as nested within host species due to the lack of any overlapping parasite species among host fishes (Figure 2), as well as distinct trajectories for each of the studied fish species (Figure 7).

PRIMER 7.0.13 was also used to generate pairwise Bray-Curtis similarity indices for all pairs of infracommunities. These similarity indices were arrayed as a triangular similarity matrix that were then used in unconstrained ordinations (two- and three-dimensional nonmetric multidimensional scaling (nMDS)) to graphically explore how parasite infracommunity structure related to host species, life stage, size, sampling locality (Clarke & Gorley 2015). Nonmetric multidimensional scaling is an unconstrained

ordination technique where proximity implies community similarity (Clarke & Gorley 2015). Multivariate analyses using PERMANOVA in PRIMER-E were used to statistically compare the effect size / significance of these factors in the shaping of parasite infracommunity structure. As explained above, all analyses considered the infracommunity as being nested within hosts.

The relative effects of host standard length, size class, and location (nested within species) on mean observed species richness were assessed using least squares regression in JMP (v. 12.1.0; SAS Institute Inc.). Preliminary model building indicated that the best combination of predictors were host size class and location, based on comparisons of the Akaike Information Criteria (AICc = 1220; all other combinations $1255 \geq AICc \geq 1363$). Consequently, host standard length was excluded from further analysis. Effects of host size class and location (nested within species) on parasite community composition and structure were assessed in PRIMER 7.0.13. Parasite communities differed among fishes, with few overlapping species; consequently parasite abundance data was summed to higher taxonomic levels (Monogenea, Digenea [adult, metacercariae], Cestoda, Acanthocephala, Nematoda [larval, adult], Copepoda, Isopoda), and pairwise Bray-Curtis similarity indices calculated for all pairs of hosts. PERMANOVA was used to test for effects of host size class and location (within species). This data was graphically represented using multidimensional scaling (nMDS).

Results

Observed species richness (OSR) varied among fish species (Table 2). White Mullet showed the highest community diversity and Atlantic Needlefish showed the lowest. Parasite communities displayed strong species specificity with only four species of parasites, three immature species, *Contracecum* sp., *Ascocotyle* sp., and Metacercariae sp., and one adult species, *Gnathia* sp., which displayed any overlap across host fishes (Figure 2). ANOSIM found no significant similarities between any of the host parasite communities ($R^2 = 0.434$, $p = 0.1$) when species was fully nested within location and size class. Variation in species richness across all host species was significant when species was nested in location and size class ($R^2=0.65$, $F_{17/339}=35.92$, $p<0.001$).

Observed species richness had a positive correlation with standard length in all host species (Figure 3). Parasite species richness showed a general increase with each location shift in all species with the exception of *M. curema* and *G. cinereus*. *G. cinereus* showed general increase between the mangroves and the inshore seagrass beds, but little to no increase when moved off to the reefs. *M .curema* showed a positive correlation between OSR and location, but did not for OSR and standard length. Although the OSR has generally higher in the reef populations the fish in the reef were smaller than those in the inshore seagrass beds, showing that this species may transition back into juvenile environments after sexual maturation.

Parasite community structure varied among all host species. The abundance of parasites, at the family level, differed over each location with most of the families showing a positive correlation with location (Figure 4). The only parasite families that did not follow this trend were adult trematodes (i.e., monogenea and digenea) which decreased in abundance at the third location (reef). Abundance of parasites at the family level also differed when compared to fish size class (Figure 5). Half of the families showed a positive correlation with size classes. The other half increased in abundance until the second or third size class and then dropped off in the four (largest) size classes. The species that decreased with size class were within the class trematode including both the immature metacercariae and the adult digenea and monogenea.

Location and size class were compared to determine which factor was influencing parasite community structure. The least squares regression model was significant (R^2 = 0.415; $F_{5/334}$ = 47.34; $p < 0.001$), with location having a stronger effect size than host size class (location: LogWorth 30.110, F-ratio 85.938, $p < 0.001$; host size class: LogWorth 8.223, F-ratio 14.586, $p = 0.001$). PERMANOVA found significant effects for location (pseudo-F 3.252, p=0.003) but not size class (peudo-F 1.76, $p = 0.077$). Analyses were nested by species and the species by location interaction was significant (pseudo-F 4.651, $p = 0.001$), indicating that at least some host species differed in how their parasite communities varied throughout their ontogenetic shifts (Figure 6).

While location was a significantly larger factor (Pseudo-F=3.25, p=0.003) than size class (Pseudo-F=1.76, p=0.077) when determining the component parasite communities across all fish species, the effect of species was the most significant (DF=2, Pseudo-F=9.18, p<0.001). This shows that the parasite community structure was driven largely by the host species itself and that each fish species should show different effects of location and size range on those communities. *C. hippos* showed a significant effect for size range (F-ratio=6.90, p<0.001), but not for location (F-ratio=1.44, p=0.25). Both *M. curema and S. barracuda* showed a significant effect for location ($F\text{-ratio}_{mul}$=38.22, p_{mul}<0.001; $F\text{-ratio}_{bar}$=3.06, p_{bar}=0.05), but *S. barracuda* did not show a significant effect for size range (F-ratio=1.47, p=0.23), and while size range did show a significant effect for *M. curema* (F-ratio=7.92, p<0.001), it was not as significant as location. The remaining two fish species of *G. cinereus,* and *S. marina* both showed a higher effect of location ($F\text{-ratio}_{moj}$=0.60, p_{moj}=0.44; $F\text{-ratio}_{ndl}$=0.56, p_{ndl}=0.58) than size range ($F\text{-ratio}_{moj}$=1.46, p_{moj}=0.24; $F\text{-ratio}_{ndl}$=0.06, p_{ndl}=0.98), but neither factor was significant. When the trajectories of each host parasite community were compared host fishes were divided into three broad response groups: one including *M. curema*, another including *S. barracuda, C. hippos*, and the final group including *S. marina*, and *G. cinereus* (Figure 7). Based on the locations of these response groups it is suggested that *M. curema* has the most distinct parasite community at all locations.

Table 2. Morphometric and parasite sample data for the five collected fish species, with number of fishes processed (N), ranges of standard length (SL), given in centimeters, and wet weight (WW), given in grams. Also shown are the total number of parasite species found in each fish (S, or overall species richness) and mean overall parasite species richness (MoSR ± SD).

Host Species	**N**	**SL (Range)**	**WW (Range)**	**S**	**MoSR**
Sphyraena barracuda	84	7 - 112	3 – 10100	16	1.3 ± 1.5
Caranx hippos	59	5 - 66	3 – 6400	20	2.4 ± 2.2
Gerres cinereus	60	2 – 22	0.04 - 352	12	1.3 ± 1.3
Strongylura marina	49	5 - 72	0.3 – 700	8	0.46 ± 0.84
Mugil curema	90	4 - 26	1 – 321	26	2.4 ± 1.6

Figure 2. Visual representation of all identified parasite species in the five sampled host fishes. Parasite abundances were transformed to the fourth root. Darker shades indicate a larger abundance of that parasite species and a lighter color indicates a lower number of parasites. Parasite species names and descriptions can be found in Appendix 2

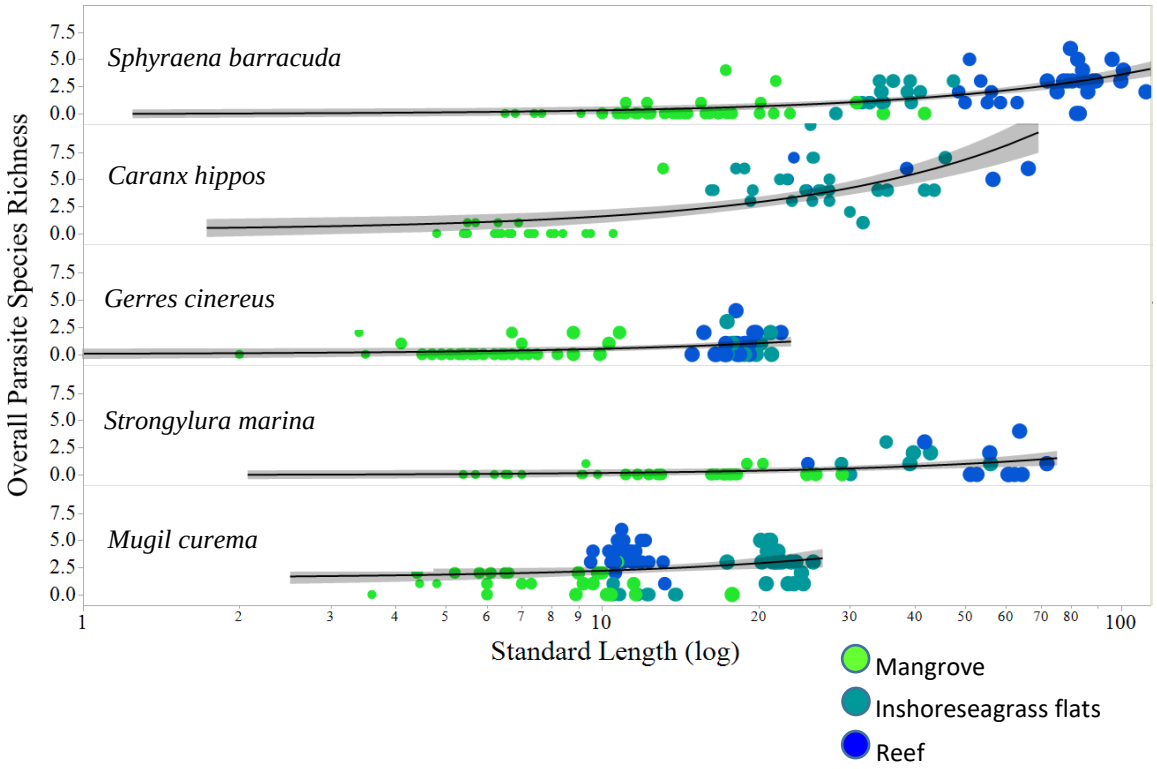

Figure 3. Parasite species richness vs log standard length of the five fish species. Standard length (cm) was significantly positively correlated with parasite richness for all five species. Color of symbol indicates sample location (green: mangrove, teal: inshore seagrass flats, blue: reef). Size of symbol indicates size class of individual fish.

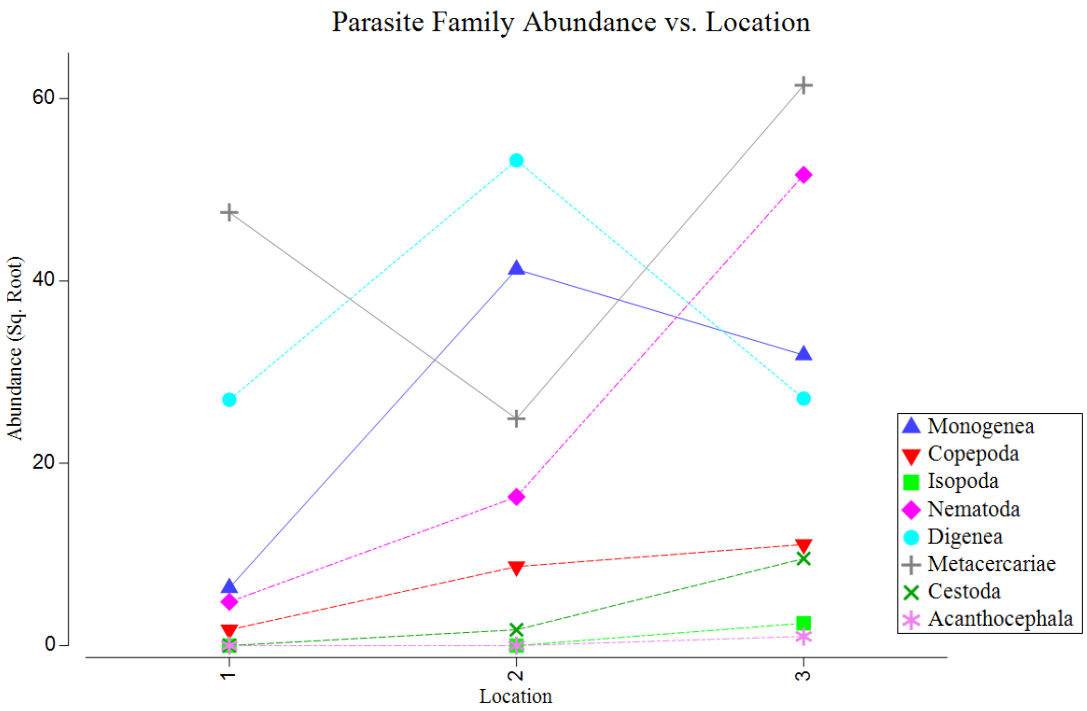

Figure 4. Change in the parasite taxa abundance, transformed by square root, versus the three sampled locations: mangrove (1), inshore seagrass flats (2), and nearshore reef (3). Individual parasites were summed to the family level. Symbol color and shape as well as trajectory color denotes parasite family. Vectors show the change in parasite abundance across habitat shifts.

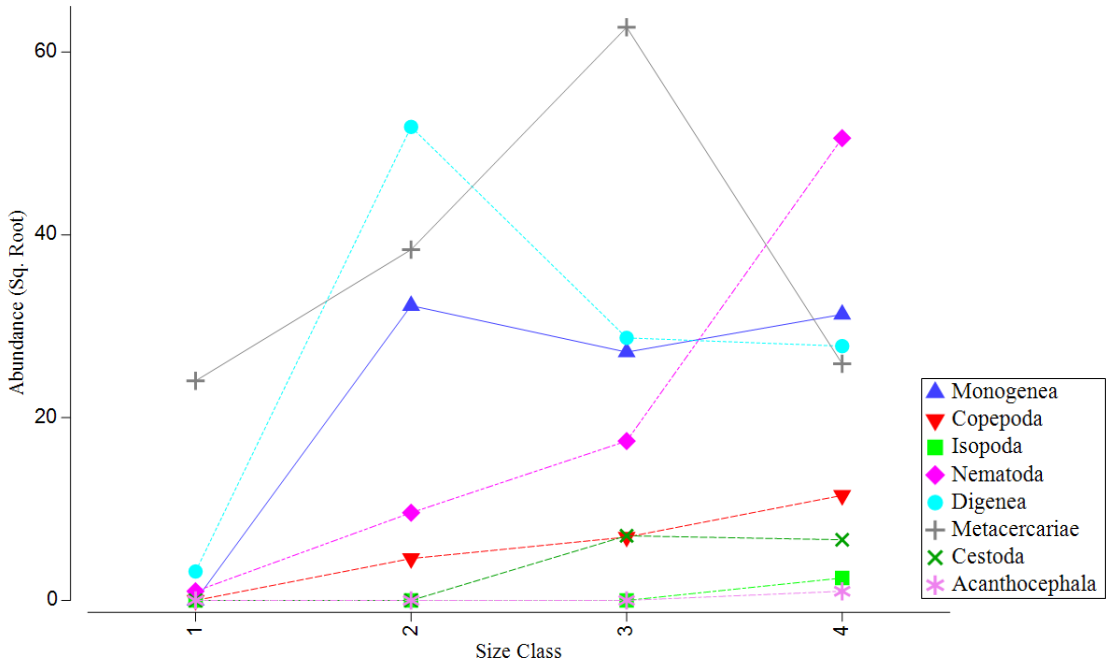

Figure 5. Change in the parasite taxa abundance, transformed by square root, versus the four size classes of sampled fish. Size classes were determined by non-metric MDS clustering, see Appendix 2. Individual parasite species were summed to the family level. Symbol color and shape as well as trajectory color denotes parasite family. Vectors show the change in parasite abundance across habitat shifts.

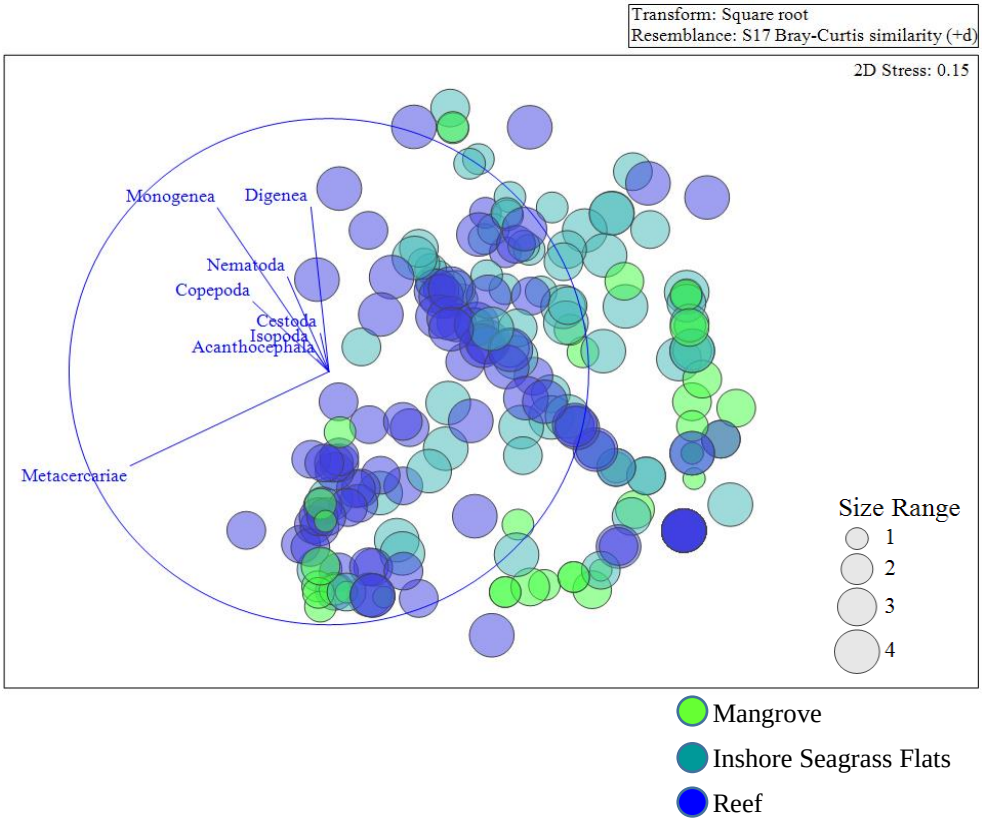

Figure 6. Nonmetric MDS of parasite community similarity among individual host fishes. Proximity of data points indicates strong similarity in parasite community composition and structure. Symbol color indicates location (green: mangrove, teal: inshore seagrass flats, blue: nearshore reef), while symbol size indicates host size range Overlay vectors indicate Pearson correlation for all parasite taxa.

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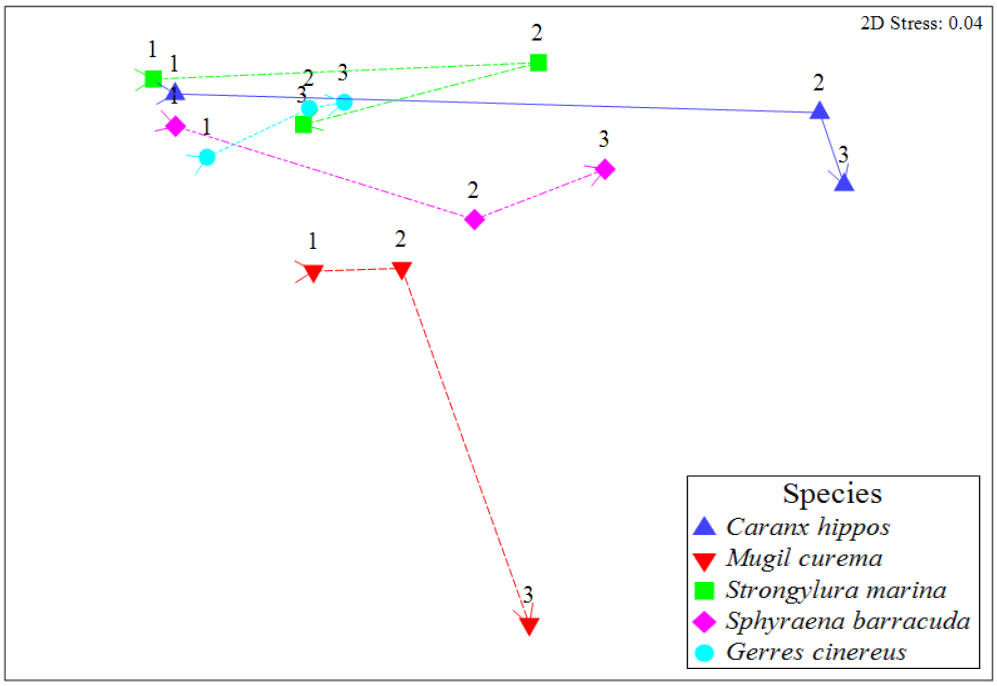

Figure 7. Nonmetric MDS of parasite community similarity among centroids for each fish species at each location. Bray-Cutris data square root transformed. Labels denote species. Symbol and vector colors denote species. Overlay arrows indicate migratory sequence, from mangrove (1) to inshore seagrass flats (2) to the nearshore reef (3). The 2D stress shows the how much the graph has been distorted to appear in two dimensions.

Discussion

Paraite Species Richness

The parasite communities within each fish species varied greatly but were otherwise distinct, with little to no parasite species overlap across the five species (Figure 2). Most of the parasite species identified were considered specialist since they only infected one of the studied host fishes. There were four parasite species that were considered generalists taxa and were found in more than one species. They include *Gnathia* sp., *Ascocotyle* sp. metacercariae, *Metacercariae* sp., and *Contracecum* sp. Metacercariae sp. and *Contracecum* sp. were found in all five species fish species. Of the four species only one, *Gnathia sp.*, was in its adult stage. This parasite could not be identified to species because identifying characteristics are only found on males that are considered free living and do not occur on fishes. All identified *Gnathia sp.* individuals were female and are considered to be the same species for the scope of this study. The three other species of overlapping parasites were all immature. This shows that the recorded hosts were used by these parasites as an intermediate host. Considering that Metacercariae sp., Ascocotyle sp. metacerariae, and Contracecum sp. are common in the South Florida area and are all generalists it is possible that all individuals, of their respective genus's, are the same species, but identifying characteristic were undistinguishable due to immaturity.

The parasite component communities, all of the parasite species infecting a population of hosts and the parasite infracommunities, the sum of all parasites infecting a single host (Bush et al. 1997) varied across all species (Table 2). *M. curema* harbored the highest compoenent community richness with 26 different parasite species present across all locations with C. hippos following closely behind with 20 identified species. *S. marina* showed the lowest with 8 parasites species identified. *M. curema* and *C. hippos* displayed the highest infracommunity richness with an average of 2.4 parasite species present in each individual fish.

Parasite Community Structure

The parasite infracommunities varied significantly with distinct subsets of parasites families in each location. This data suggest that as the populations of fish age and begin their ontogenetic habitat shifts to the reefs, they not only tend to acquire a higher abundance of parasites but also a higher overall parasite species richness. Both location and size range also played a significant role in the composition of parasite communities overall. Of the two factors, location was found to play the more significant role showing that the parasite infracommunity in each fish was directly related to the environmental and trophic interactions that were acquiring within their habitat, as well as the habitats that they had previously encountered. The higher effect of location also shows that the three habitats themselves were distinctly different in the parasite component community composition across all species.

Location as a Factor: Mangrove Habitats

Parasite species found in the mangrove environment were very limited, with many of the individual fish being uninfected. Most of the observed parasites were trematodes, and included monogenean species and immature encysted digeneans. These taxa are considered to be penetrating or contagious parasites, using transmission modes that are likely favored by the physical environment in the mangroves, as stated above. In addition to the contagious parasites, there were few trophically-acquired parasites found in fishes in the mangrove habitat. Trophically-acquired parasites are those that are ingested by a host species either directly, or through consumption of an infected intermediate host (Marcogliese 2002). These trophically-acquired parasites were restricted to a very low abundance of adult digeneans and immature encysted nematodes. The diet of fishes in the mangrove environment, consisting mainly of detritus and plant material at this life stage, likely limits the opportunity to acquire trophically-acquired parasites. It is possible that these fishes are acquiring these trophically-acquired parasites incidentally or intentionally through the ingestion of eggs and cysts on vegetation or floating in the water column (Holmes & Price 1980).

There are many potential reasons that many of the juvenile fishes examined from the mangroves had few or no parasite species present (Figure 3). For example, fishes may

not have been in the environment long enough to acquire parasites or may not have been in the environment during peak infection stage presence. Parasite acquisition is directly related to the rate of interaction between infective stage parasites and/or trophic interactions therefore the chance of parasite acquisition should be positively correlated to the amount of time spent in the environment (Poulin 1995). Even though they had a large abundance of digenea metacercariae it cannot be known for sure that they acquired these parasites in the mangrove habitat. Since these encysted parasites stay in the fish until host death or until the host produces a large immune response it is unclear whether these parasites were acquired in the mangrove environment or during their initial movement from the reefs in to the mangroves as premetamorphized fishes (Alvarez-Pellitero 2008). Many fishes that undergo ontogenetic habitat shifts begin their movements only days after settlement in the mangrove habitats, which limits their exposure to parasite propagules in nursery habitats (Nagelkerken et al. 2002). The longer a juvenile fish spends in an environment with infectious stage parasites present, the greater the chance of the fish coming into contact with them and becoming infected (Poulin 1995). Mortality rate of post-settlement juvenile fishes is extremely high (>61%) and increases further if the fishes acquires a parasite infection (Nagelkerken et al. 2002). The decrease in fitness due to any level of infection, especially a high one, could lead to a higher mortality rate caused by the inability to avoid predation, incapacity to compete for necessary resources, incapability to overcome the physiological demands caused by the infection, and the lack of a developed immune response to the pathogen (Altizer et al. 2011). Regardless of the indirect or direct cause, these juvenile fishes would have been removed from the environment before they would have been able to be sampled. In addition to mortality, the physical size of these individuals may play a role in the low parasite diversity as well. Juvenile fishes, many being only a couple of centimeters in length, do not have many physical niches within or on their bodies, nor space within those niches to be able to maintain a mature parasite community (Poulin 1995).

The theories of migratory escape and migratory culling may play a role in the limited abundance of parasite species within the mangrove habitat. Migratory escape occurs when uninfected individuals migrate, or in the case of this study initiate their ontogenetic habitat shift, in response to high levels of parasite contamination within the

environment (Altizer et al. 2011). The high abundance of contagious parasites in the mangrove habitats may be forcing the juvenile fishes to begin their shift prematurely to escape before they become infected. This initiation of movement of healthy individuals to leave a highly infectious environment is known as migratory culling (Hall et al. 2014). This theory states that movements can lower the pathogen prevalence by removing infected individuals from the populations. Hosts that are heavily infected would be less likely to migrate due to the physiological demands that accompany these movements (Altizer et al. 2011). Even if infected individuals were to attempt migration they would not be able to move as far and as quickly as their uninfected conspecifics, thereby resulting in a higher rate of mortality (Altizer et al. 2011). The effect of migratory culling and escape should show a significant effect in the parasite communities in the inshore seagrass beds and the reef environments by removing infected individuals from the habitats.

Location as a Factor: Inshore Seagrass Bed Habitat

Fishes that initiated ontogenetic habitat shifts and transitioned into the inshore seagrass beds showed a significant increase of abundance in both individual parasites and overall parasite species richness. Fishes moving out of the mangrove environment lacked significant parasite infection, thus inferring that the fishes transitioning into the seagrass beds acquired the parasites rapidly when introduced to the infectious stage pathogens associated with their new environment (Poulin 1995). The fishes transitioning into the seagrass beds were also larger in size than their conspecifics in the mangrove habitats, allowing for even more available space within the almost empty niches. Rapid parasite acquisition is essential for the progression and maturation of the parasite infracommunities and is known as the non-interactive phase (Holmes & Price 1980). The non-interactive phase of community development occurs when there are large amounts of resources available and unexploited, and there are small numbers of individuals relative to carrying capacity. The increase of parasite individuals initially allows for the coexistence of different species exploiting the same resources within the host, which should show increased parasite diversity in newly transitioned fishes (Holmes & Price 1980).

Unlike the parasites found in the mangrove habitat most of the parasites identified in the seagrass beds were in their adult stages (Figure 4). The shift to an adult parasite dominance shows that many of the fish species transitioned from being the intermediate hosts to the definitive hosts. The sub-adult fishes are thought to make this transition based on the known parasite life cycle that states that any host that harbors a larval or immature stage parasite is considered an intermediate host and any host that harbors a sexually mature adult parasite is considered a definitive host (Despommier & Karapelou 2012). This shift to a definitive host was exclusive to parasites that utilize intermediate and definitive hosts within their lifecycles. The decrease in digenean metacercariae from the mangrove to the seagrass habitats shows this transition distinctly. As the fish move out of the environment containing infectious stage parasites and intermediate hosts into an environment lacking these, they break the infection cycle. Parasites that are direct penetrators, as well as those that rely on intermediate hosts, decline in abundance in response to movement (Alitizer et al. 2011). If there are no intermediate hosts to produce infective stages (e.g., cercariae) in the new environment, then the life cycle of the parasite is interrupted (Alitizer et al. 2011). The decrease in digenea metacercariae may also be explained by migratory escape and migratory culling; if so, only the fishes with low metacercariae infection rates or no infection at all would be able to complete their habitat shift to the seagrass beds. A high infection rate has been shown to force fishes to postpone their habitat shift or cause them to make an unsuccessful attempt at one, which leads to the culling of many infected individuals in the mangroves instead of in the seagrass beds (Alitizer et al. 2011).

Aside from the decrease in digenea metacercariae, all other parasite families increased in abundance in the seagrass beds, including the addition of parasites from the families copepoda and cestoda. The additional parasite diversity can be explained by an ontogenetic diet shift that accompanies habitat shift as well the addition of new predator prey interactions within the seagrass beds (Table 2). Each new habitat that the individual fish transition through should, by definition, also bring a new subset of parasites due to the new interactions that occur between the fish and the environment (Poulin 1995). Significant increases in trematoda diversity was also seen, with the larger increase from adult digenea. The transition into the seagrass beds increases physiological demands on

the fishes thus forcing them to undergo a diet shift from mostly detritus and plant material to small fishes and crustaceans (Altizer et al. 2011). This dietary shift allows for of the addition of trophically-acquired parasites that use small fishes and crustaceans as intermediate hosts, thus transitioning the sub-adult fishes to definitive hosts of these parasites (Poulin 1995). The physiological stress of movement also forces the individual fish to consume more resources, thus increasing the chance of ingesting an infected intermediate host (Altizer et al. 2011).

For the fishes in this study, multiple areas within the seagrass beds are used as "stopover" sites during their movements, which are areas used by multiple species as a place to rest and feed before continuing their transition into the reef habitats (Altizer et al. 2011). Due to the increased number of conspecific and heterospecific fishes that make use of these areas, there is a large abundance of infectious parasites (Altizer et al. 2011). Stopover sites are ideal habitats for both contagious parasites, which can be passed easily from individual to individual through direct contact and short bursts of swimming (e.g., monogenea and copepoda) (Altizer et al 2011). The increased feeding rate at stopover sites also show an increase in trophically-acquired parasites. It is in these areas that parasite communities tend to enter the interactive phase of parasite community maturation, where parasite within the fish start interacting and competing with one another for resources with one another causing the overall species richness to decrease (Holmes & Price 1980).

Location as a Factor: Reef Habitats

Fishes on the reefs were found to have the highest abundance of parasite and overall parasite species richness. Once the fishes moved onto the reef habitats, their parasite communities appeared to mature as individuals from all local parasite families were present. The movement from the inshore seagrass beds to the reefs show the assertive phase, where colonization and extinction of parasite species occur simultaneously into particular niches and locations that allow the community to co-exist more effectively (Holmes & Price 1980). Transitions towards co-existence within the parasite community can be seen most clearly with the decrease of adult trematoda in the reef environment. In the mangrove and inshore seagrass beds, the adult trematoda were

dominant due to lack of presence from other parasite families. Once they complete their habitat shift to the reef habitat, individual fishes begin feeding on larger prey due to their increased size as well as the higher abundance of available resources, simultaneously exposing them to a new variety of potential pathogens within the environment (Altizer et al. 2011).

Aside from all species of adult trematoda, specifically the species in the families digenea and monogenea, all other families of parasites increased in abundance and species richness within the reef habitat. The addition of the families isopoda and acanthocephala can be seen further showing the maturation of the parasite community. The decrease in monogenea could possibly be due to the competition for resources in the gill filaments between them and the various species of copepoda and isopoda that are newly introduced in the reef habitat.

Host Species as a Factor

Host species was found to be the most significant factor effecting the parasite community structure of these fishes. This shows that the fish species itself and its interactions with the environment, both physically and trophically directly affected the parasites in which it became infected with. When the host fish species were analyzed by their parasites communities, each of the five fish followed one of two characteristic responses (Figure 7). The first was followed by *S. barracuda, S. marina, C. hippos*, and *G. cinereus*, and all four species had communities that were similar in the mangrove habitats with few to no parasites at all. The transition to the inshore seagrass beds shows a distinction between the species that underwent early diet shifts and the ones that do not. The three fishes that transitioned into a piscivorous diet – i.e., *C. Hippos*, *S. marina* and *S. barracuda* – all showed an increase in abundance and species richness that distinguished it from the communities of the other species. These fishes showed a much smaller change in community structure between the seagrass beds and the reef habitats with *S. marina* showing a relative decrease in community structure which transitioned their parasite community into one more similar to the parasite community in the mangrove habitat than the inshore seagrass beds. This small shift in parasite community structure may show the initial diet shift that occurs in the beginning of the transition out

of the mangroves causes the largest parasite community change. Both *S. barracuda* and *C. hippos* continue to feed higher on food web as they grow thus continuing to increase the diversity within their parasite communities. *S. marina*, on the other hand continues to feed on small fishes and crustaceans even as they grow which allows them to maintain a mature parasite community with limited parasite species that are constantly battling the immune response of the individual. *G. cinereus* showed only a small jump in parasite diversity between the mangrove and the seagrass beds and an even smaller change in the community from the seagrass beds to the reefs. Once *G. cinereus* individuals transition from feeding on detritus and plant material to feeding on benthic invertebrates, they only revert back to plant material if food is scarce. (Zahorcsak et al. 2000). The diet of mostly plant material and invertebrates, like *S. marina*, allows *G. cinereus* to keep a relatively low number of parasites in their infracommunities. The diet, overall, shows a possible explanation for *why S. marina* and *G. cinereus* showed relatively little change in their parasite community structure over the course of the ontogenetic habitat shift.

In contrast, the parasite community of *M. curema* displayed a different pattern then the other four fish species, with a higher abundance of parasites at all locations including the mangrove habitats. As individuals transition between habitats, they continue to acquire new parasites, most significantly during the transition between the mangroves and the seagrass beds. Since *M. curema* feeds at a much lower trophic level then all of the other fishes in this study, examined individuals also showed a distinctly different parasite community. Finally, *M. curema* completes seasonal migrations or "runs" that constantly have them entering and exiting different environments, which could explain the extremely high parasites species richness found in this species.

Based on these distinctions it can be proposed that diet could play a role in the parasite community structure of these fishes. A possible factor affecting overall species richness throughout the ontogenetic habitat shift could be the difference in the feeding dynamics of each species, especially considering that trophic interactions are critical in the acquisition of parasites (Knudsen et al. 2004). All of the species undergo dietary trophic shifts in association with their ontogenetic habitat shifts (See Table 2), with the exception of *M. curema* (Abaraca-Arenas 2014). Since location was a significant factor in the composition of parasite communities and the diet of each fish species was found to

change at each location, to varying degrees, it is possible the diet of the individual was also a significant factor in the parasite community composition.

Host Size as a Factor

Another factor that explains the distinction in effect factors could be the rate of growth of the fish. As shown in Figure 2, most of the fish species demonstrated that an increase in size was directly related to increase in parasites (even if only slightly). The two species that fit the pattern best were *S. barracuda and C. hippos*, which also have the largest size range variation of sampled individuals. The fish that had the least fit to the model was *M. curema.* In the case of *M. curema*, it appear as if most of the growth occurs at the beginning of the transition and size is somewhat maintained throughout the life of the fish. Fishes sampled from the inshore seagrass beds were larger than those in the reef environment. The lack of size distinction between the habitats shows that *M. curema* moves in between both habitats regularly, possibly in search of food and/or avoiding predation. This explains the highly significant effect of location because even the smaller individuals from the reef environment had a higher parasite abundance then there conspecifics of larger size in the inshore seagrass beds. *C. hippos* is the only species that shows a large increase is size related to parasite species richness. The larger individuals in both the reef and the inshore seagrass bed showed a much higher parasites species richness then other species in the same location (Figure 2). Individuals in both the inshore seagrass beds and the reef habitat had very similar parasite species richness with the largest parasite abundance being found in the seagrass beds.

Future Research

Little research has been conducted on the physiological effects of parasitic infection, more specifically the critical parameters such as respiratory function or energy cost of infection in fishes. Altizer et al. (2011) proposed that migrating individuals showed an increased immune response at the beginning of movement, but were likely to be susceptible to a large parasitic infection towards the end of their movement due to the respiratory demands of the migration. Experimentally infecting of individual fishes and then stress testing them could give insight on the effect of these parasites on the fishes

physiologically. Also, capturing infected juvenile fishes and observing them in a controlled environment over an extended period of time could aid in determining whether these fishes create an adaptive immune response over time against the parasite (Scott 1986).

Future studies should continue to look at location instead of size as the main variable in parasite acquisition. To further the distinction of location as a factor of parasite acquisition similar studies should be done in all three of the environments separately to determine how the parasite community structure changes in fishes that recide in that environment. Also, parasite community structure should be researched on intermediate hosts throughout these environments. Since all of the parasite families identified in this study (see Appendix 2) with the exception of Monogenea and Copepoda use intermediate hosts it could show how the abundance of intermediate hosts in the environment affected the abundance of parasites within that environment. This, along with, more extensive gut content analysis should be done to determine the critical roles of these parasites within the ecosystem. It has been suggested that diet is directly related to the abundance of trophically acquired parasites (ie. Digenea, Cestoda, and Acanthocephala) (Arneburg et al 1998). Gut content analysis would aid in determining if consumption of specific prey species could be linked to the parasites infecting the fishes. Other factors such as position in the water column and fish behavior, if studied, could give an interesting interpretation of parasite infection in the ecosystem. Alitizer et al. (2011) previously suggested that fishes that demonstrate schooling behavior are more likely to become infected by their conspecifics but contagious and direct penetrating parasites (e.g. Monogenea and Copepoda). Future studies on this topic could aid in explaining the adaptive behavior of contagious parasites that infect fishes that demonstrate school behaviors. The anthropogenic effects on parasite communities and environment should also be studied. Different parasite taxa react differently to anthropogenic effects therefore this could be driving the presence/absence of parasites in these environments. The definitive and intermediate hosts in these environments also react differently to anthropogenic effects, so this could also be affecting the abundance of parasites (Morley 2007). Overall, there is much more that needs to be looked at to

determine why location play such a large factor in the composition of parasite communities in these fishes.

Conclusions

The purpose of this study was to determine the effect of habitat on the parasite communities within five common fish species in South Florida that undergo ontogenetic habitat shifts between mangroves, seagrass beds, and reefs. Location was the largest driving factor in the composition of parasite communities, and it was found that the reef environments had the highest abundance and diversity of parasites out of all three habitats. The adults of all of these species spawn offshore and then the larval fishes migrate into the mangrove areas. This recruitment pattern into the mangroves occurs for a variety of hypothesized reasons, including avoiding predation, habitat complexity, and an increased amount of available resources (Snover 2008). Based on this study, another driving reason that these larval fishes recruit into the mangrove habitats may be to avoid parasite acquisition during a critical developmental stage. Poulin et al. (2012) proposed that migration into nursery or juvenile habitats was driven by the need for developing fishes to be in an environment with low parasitism during their critical developmental stages, where they are extremely susceptible to mortality by parasitism. Since mortality is already very high in all species of larval teleosts, it is critical that these juvenile fishes are in as environment with low parasitism to minimize the potential of mortality. Once these juvenile fishes are larger and stronger they being their ontogenetic habitat where they gradually acquire more parasites until they eventually complete their shift to the reef habitats. This risk of the movements, both the transition from the reef to the mangroves as larval fishes and the transition back to the reef as sub-adults must significantly outweigh the cost and possible mortality. In the case of the initial transition to the mangroves the risk of mortality during the shift is significantly lower than the imminent mortality by parasite infection or predation on the reefs. Once the fishes have matured passed their critical developmental stage, they begin the habitat shift back to the reefs where the risk of mortality by the acquisition of parasites is outweighed by the reward of

residing in a more productive environment with a larger amount of available resources as well as the reward as spreading their genes through reproduction.

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Appendix 1: Previously described parasites of studied fish species

Table of all known parasite species previously identified in the five fish species studied including the site of infection in the host as well as the geographic region in which the host was sampled. Geographic range has emphasis on the Southeastern Region of the United States and well as the Gulf of Mexico and Caribbean Sea, but all known ranges of the parasite species were included.

Abbreviations used throughout the table: bcv = body cavity; mou = mouth; nas = nasal cavities; eye = eye; fin = fins; gbd = gallbladder; gil = gills; hrt = heart; int = intestine; liv = liver; pcc = pyloric ceca; sbd = swim bladder; sto = stomach; gon = gonads; spl = spleen; wvs = wall of viscera; ext = external; sub = subcutaneous; mus = muscle; brn = brain

AO = Arctic Ocean; BE = Bermuda; CS = Caribbean Sea; EA = eastern Atlantic Ocean; EP = eastern Pacific Ocean; GM = Gulf of Mexico, IO = Indian Ocean; NE = northeastern United States and Atlantic Canada; SA = Atlantic coast of South America; SE = southeastern United States and the Bahamas; and WP = western Pacific Ocean; HI = Hawaii; MS = Mediterranean Sea

Taxon	Host	Site in Host	Geographic Range	Reference
Phylum: Acanthocephala				
Class: Eocanthocephala				
Order: Neoechinorhynchida				
Family: Neoechinorhynchidae				
Floridosentis elangatus Ward, 1953	*Mugil curema*	int	SE, GM, CS, EP	Oren 1981
Floridosentis mugilis (Machado Filho, 1951)	*Mugil curema*	int	CS	Bunkley-Williams & Williams 1994
Floridosentis pacifica Bravo-Hollis, 1969	*Mugil curema*	int	EP	Overstreet 1981
Class: Palaeacanthocephala				
Order: Echinorhynchida				
Family: Isthmosacanthidae				
Gorgorhynchoides bullocki Cable & Mafarachisi, 1970	*Sphyraena barracuda*	int	CS	Monk et al. 2009
Gorgorhynchoides alongatus Cable & Linderoth, 1963	*Caranx hippos*	int	GM, CS, SE	Bunkley-Williams & Williams 1994

Phylum: Annelida				
Class: Clitellata				
Order: Rhynchobellida				
Family: Piscicolidae				
Myzobdella lugubris (Leidy, 1851)	*Mugil curema*	ext	NE, SE, CS, GM	Oren 1981
Phylum: Arthopoda				
Class: Hexanauplia				
Subclass: Copepoda				
Family: Bomolochidae				
Acantholochus crevalleus (Cressey, 1981)	*Caranx hippos*	gil, nc	SE, GM	Bunkley-Williams & Williams 1994[1]
Bomolochus bellones Burmeister, 1833	*Strongylura marina*	gil	EP, GM, SE	Morales-Serna et al. 2012; Cressey & Collette 1970
Family: Caligidae				
Caligus bonito Wilson C.B., 1905*	*Mugil curema*	gil	SE, GM	Morales-Serna et al. 2016
Caligus chorinemi Krøyer, 1863	*Caranx hippos*	gil	SE, CS, GM	Bunkley-Williams & Williams 1994
Caligus constrictus Heller, 1865	*Caranx hippos*	gil	EP	Moravec & Bakenhaster 2012
Caligus coryphaenae Steenstrup & Lütken, 1861	*Caranx hippos*	gil, ext	NE, SE, CS, GM	Bunkley-Williams & Williams 1994
Caligus diaphanus von Nordmann, 1832	*Caranx hippos*	ext	GM	Love & Moser 1983
*Caligus elongatus*von Nordmann, 1832	*Caranx hippos*	ext	NE, SE, GM	Bunkley-Williams & Williams 1994
Caligus isonyx Steenstrup & Lütken, 1861*	*Sphyraena barracuda*	ext, gil, mou	SE	Skinner 1978
Caligus lobodes (Wilson C.B., 1911)*	*Sphyraena barracuda*	ext, gil, mou	SE, CS, GM	Morales-Serna et al. 2016
*Caligus longipedis*Bassett-Smith, 1898	*Caranx hippos*	ext	SE, GM	Bunkley-Williams & Williams 1994
Caligus pomacentrus Cressey, 1991	*Mugil curema*	gil	SE, CS	Bunkley-Williams & Williams 1994
Caligus praetextus Bere, 1936	*Caranx hippos*	gil	GM	Love & Moser 1983

Caligus productus Dana, 1852*	*Sphyraena barracuda*	mou, gil	SE, GM	Bunkley-Williams & Williams 1994
Caligus robustus Bassett-Smith, 1898	*Caranx hippos*	ext, gil	GM, SE	Hayes et al 2012
Caligus rufimaculatus Wilson C.B., 1905	*Sphyraena barracuda*	ext, gil	SE, GM, CS	Morales-Serna et al. 2016
Caligus spinosus Yamaguti, 1939*	*Caranx hippos*	gil	SE	Bunkley-Williams & Williams 1994
Caligus tenax Heller, 1865	*Caranx hippos*	gil	SE	Pearse 1951
Leopeophtheirus edwardsi Wilson, C.B., 1905	*Caranx hippos*	ext	NE	Bunkley-Williams & Williams 1994
Tuxophorus caligodes Wilson C.B., 1908	*Caranx hippos*	ext	SE, GM	Bunkley-Williams & Williams 1994
Family: Ergasilidae				
Acusicola rogeri Amado & Rocha C.E.F., 1996	*Strongylura marina*	gil	SA	Pinto da Motta Amado & Falavigna da Rocha 1996
Acusicola tenax (Roberts, 1965)	*Strongylura marina*	gil	SA	Amado et al. 1996
Ergasilus arthrosis Roberts, 1969	*Strongylura marina*	gil	SE	Roberts 1969
Ergasilus atafonensis Amado & Rocha, 1997	*Mugil curema*	gil	SA	Amado & Rocha 1997
Ergsailus bahiensis Amado & Rocha, 1997	*Mugil curema*	gil	SA	Amado & Rocha 1997
Ergasilus caraguatatubensis Amado & Rocha, 1997	*Mugil curema*	gil	SA	Amado & Rocha 1997
Ergasilus ecuadorensis El-Rashidy & Boxshall, 2002	*Mugil curema*	gil	GM	El-Rashidy & Boxshall 2002
Ergasilus lizae Krøyer, 1863*	*Mugil curema*	gil	SE	Wilson 1911
Ergasilus mugilis Vogt, 1877*	*Mugil curema*	gil	CS	Bunkley-Williams & Williams 1994[2]
Ergasilus spatulus Cressey in Cressey & Collette, 1970	*Strongylura marina*	gil	SE	Cressey & Collette 1970
Ergasilus vericolor Wilson C.B., 1911	*Mugil curema*	gil	SE	Wilson 1911
Family: Hatschekiidae				
Hatschekia amplicapa Pearse, 1951	*Sphyraena barracuda, Caranx hippos*	gil	CS, SE, GM	Bunkley-Williams & Williams 1994
Hatschekia oblonga Wilson 1913	*Caranx hippos*	gil	GM	Love & Moser 1983
Family: Pennellidae				

Lernaeenicus longiventris Wilson C.B., 1917	*Mugil curema*	gil	CS	Bunkley-Williams & Williams 1994
Lernaeolophus striatus Wilson C.B., 1913	*Sphyraena barracuda*	mou, nc	CS, SE	Bunkley-Williams & Williams 1994
Lernaeolophus sultanus (Milne Edwards, 1840)	*Strongylura marina*	gil	GM	Cressey & Collette 1970
Family: Lernaeopodidae				
Naobranchia lizae (Krøyer, 1863)*	*Mugil curema*	gil, fin	GM, SE, EP	Oren 1981; Overstreet 1981
Thysanote goodi Causey, 1960	*Sphyraena barracuda*	mou	SE, GM	Morales-Serna et al. 2016
Family: Lernanthropidae				
Lernanthropus belones Krøyer, 1863*	*Strongylura marina*	gil	SE	Cressey & Collette 1970
Lernanthropus giganteus Krøyer, 1863*	*Caranx hippos*	gil	CS	Bunkley-Williams & Williams 1994
Lernanthropus kroyeri Van Beneden, 1851	*Caranx hippos*	gil	GM	Boada et al. 2012
Lernanthropus tylosuri Richiardi, 1880	*Strongylura marina*	gil	GM	Cressey & Collette 1970
Family: Philichthtidae				
Colobomatus goodingi Cressey & Collette, 1970	*Strongylura marina*	sub, ext	SE	Cressey & Collette 1970
Class: Icthyostraca				
Subclass: Branchiura				
Family: Argulidae				
Argulus bicolor Bere, 1936	*Sphyraena barracuda*	ext	SE	Skinner 1978
Class: Malacostraca				
Order: Isopoda				
Family: Aegidae				
Rocinela signata Schioedte & Meinert, 1879*	*Sphyraena barracuda*	gil	SE, GM	Bunkley-Williams & Williams 1994
Family: Corallanidae				

Excorallana tricornis (Hansen, 1890)	*Sphyraena barracuda, Caranx hippos*	mou, gil	CS	Bunkley-Williams & Williams 1994
Family: Cymnothoidae				
Cymothoa oestrum (Linnaeus, 1758)	*Sphyraena barracuda; Caranx hippos*	gil	CS, GM	Bunkley-Williams & Williams 1994; Williams et al. 2006
Livoneca ovalis (Say, 1818)	*Caranx hippos*	gil, mou	NE, SE	Bunkley-Williams & Williams 1994
Mothocya xenobranchia Bruce, 1986	*Strongylura marina*	gil	CS, GM	Hadfiled et al. 2014; Bruce 1986
Family: Gnathiidae				
Gnathia spp. Leach, 1814*	*Sphyraena barracuda*	gil, nc	CS	Bunkley-Williams & Williams 1994
Phylum: Nematoda				
Class: Chromadorea				
Order: Rhabditida				
Family: Anisakidae				
Contraceacum multipapillatum (Drasche, 1882) Lucker, 1941	*Mugil curema*	liv, kid	GM, MS	Overstreet 1981
Contraceacum spp. Railliet & Henry, 1912	*Mugil curema, Gerres cinereus*	liv, mus	EP	Fajer et al. 2005
Pseudoterranova spp. Mozgovoi, 1951	*Sphyraena barracuda*	sub	GM	Laffon-Leal 2007
Family: Cucullanidae				
Cucullanus djilorensis Ndew, Diouf, Ba & Morand, 2014	*Mugil curema*	int	IO	Ndew et al. 2014
Family: Philometridae				
Caranginema americanum Moravec, Montoya-Mendoza & Salgado-Maldonado, 2008*	*Caranx hippos*	sub	SE, GM, EP	Moravec & Bakenhaster 2012
Philometra spp. *Costa, 1845*	*Strongylura marina*	gon	SE	Moravec & Bakenhaster 2012
Phylum: Platyhelminthes				

Class: Cestoda				
Order: Tryoanohyncha				
Family: Eutetrarhynchidae				
Dollfusiella lineata (Linton, 1909)	*Caranx hippos*	wvs	GM, SE	Bunklry-Williams & Willaims 1994[3]
Family: Lacistohynchidae				
Dasyrhynchus giganteus (Diesing, 1850)	*Caranx hippos*	mus, sto	SE, NE, GM, CS	Bunkley-Williams & Williams 1994[4]
Family: Otobothriidae				
Otobothrium dipsacus Linton, 1897	*Sphyraena barracuda*	int, bc, wvs	SE	Bunkley-Williams & Williams 1994[5]
Family: Pseudotobotriidae				
Pseudotobothrium dipsacum (Linton, 1897)	*Sphyraena barracuda*	bc	SE	Ward 1954
Family: Tentaculariidae				
Heteronybelinia estigmena (Dollfus, 1960)	*Caranx hippos*	wvs, sto, int	SE	Bunkley-Williams & Williams 1994[6]
Tentacularia spp. Bosc, 1797	*Sphyraena barracuda*	mus, wvs	CS	Bunkley-Williams & Williams 1994
Family: Tetraphyllidae				
Scolex polymorphus Rudolphi, 1819	*Mugil curema*	int	GM	Oren 1981[7]
Class: Trematoda				
Subclass: Digenea				
Family: Acanthocolpidae				
Manteria brachyderus (Manter, 1940) Caballero, 1950	*Caranx hippos*	int	EP	Manter 1940[8]; Williams et al. 1996

Stephanostomum ditrematis (Yamaguti, 1939) Manter, 1947*	*Caranx hippos*	int	GM, SE, CS, SA, EP, WP, IO	Overstreet et al. 2009; Manter 1940[9]
Stephanostomum gracile (Vigueras, 1942)	*Sphyraena barracuda*	int	GM, CS, SE	Overstreet et al. 2009[10]
Stephanostomum hispidum (Yamaguti, 1934) Manter, 1940	*Caranx hippos*	int	SE, GM, SA	Bashirullah & Aguado 2009
Stephanostomum megacephalum Manter, 1940	*Caranx hippos*	int, gil	GM, CS, EA, EP	Overstreet et al. 2009; Manter 1940
Stephanostomum sentum (Linton, 1910) Manter, 1940	*Caranx hippos*	int	CS	Bunkley-Williams & Williams 1994
Family: Apocreadiidae				
Crassicutis marina Manter, 1947	*Gerres cinereus*	int	GM, SE, CS, EP	Overstreet et al. 2009; Williams et al. 1996
Homalometron elongatum (Overstreet, 1970)*	*Gerres cinereus*	Int, occ	GM, CS, EP	Overstreet et al. 2009
Neoapocreadium gerrdis (Nahhas & Cable, 1964) Cribb & Bray, 1999	*Gerres cinereus*	int	CS	Cribb & Bray 1999
Neoapocreadium marinum (Manter, 1947) Cribb & Bray, 1999	*Gerres cinereus*	int	SE, SE, GM	Cribb & Bray 1999
Family: Bucephalidae				
Bucephalus gorgon (Linton, 1905) Eckmann, 1932*	*Caranx hippos*	sto, gil	GM, SA	Manter 1940[11], Bunkley-Williams & Williams 1994[12]
Bucephalus kaku Yamaguti, 1970	*Sphyraena barracuda*	int, pcc	HI	Bray & Justine 2011
Bucephalus margaritae Ozaki & Ishibashi, 1934	*Sphyraena barracuda; Caranx hippos*	int, pcc, ext	HI, SA, GM, CS, EA, WP, IO	Al-Zubaidy 2011, Overstreet et al. 2009, Bray & Justine 2011[13]
Rhipidocotyle barracudae Manter, 1940	*Sphyraena barracuda; Strongylura marina*	Int, pcc	GM	Overstreet et al. 2009; Manter 1947
Rhipidocotyle bartolii Bray & Justine, 2011	*Sphyraena barracuda*	Int, pcc	GM	Bray & Justine 2011
Rhipidocotyle lepisostei Hopkins, 1954	*Mugil curema*	Int	GM	Overstreet et al. 2009; Oren 1981
Rhipidocotyle lintoni Hopkins, 1954	*Strongylura marina*	int	GM	Stunkard 1976
Rhipidocotyle longicirrus (Nagaty, 1937) Bartoli & Bray, 2005*	*Sphyraena barracuda*	Int, pcc	GM, CS, IO	Overstreet et al. 2009[14]

Rhipidocotyle longleyi Manter, 1934*	*Sphyraena barracuda*	Int, pcc	GM	Overstreet et al. 2009[15]; Manter 1947[15]
Rhipidocotyle transversalis Chandler, 1935	*Strongylura marina*	int	GM	Stunkard 1976; Overstreet et al. 2009
Prosorhynchoides arcuatus (Linton, 1900) Love & Moser, 1983	*Sphyraena barracuda; Strongylura marina*	Int, pcc	GM, SE, NE, CS, SA, WP	Overstreet et al. 2009[16]; Manter 1947[16]
Prosorhynchoides attenuatus (Siddiqi & Cable, 1960) Srivastava & Chauhan, 1973	*Sphyraena barracuda*	int, pcc	IO	Bunkley-Williams & Williams 1994[17]
Prosorhynchoides gracilescens	*Caranx hippos*	int, pcc, sto	SE	Bunkley-Williams & Williams 1994[18]
Prosorhynchoides longoviferus (Manter, 1940)*	*Sphyraena barracuda; Strongylura marina*	Int, pcc	GM, CA	Overstreet et al. 2009; Manter 1947
Prosorhynchoides strongylurae (Hopkins, 1954)	*Strongylura marina*	int	GM	Overstreet et al. 2009
Prosorhunchus longicollis Yamaguti, 1953	*Sphyraena barracuda*	int, pcc	IO	Bray & Justine 2011
Prosorhynchus stunkardi Siddiqi & Cable, 1960	*Caranx hippos*	int, pcc	CS	Dyer et al. 1992
Family: Clinostomidae				
Clinostomum complanatum (Rudolphi, 1814) Braun, 1899	*Mugil curema*	fin, wvs, mou	EP, SA	Pulido-Flores et al. 2015
Family: Cryptogonimidae				
Claribulla longula Overstreet, 1969	*Sphyraena barracuda*	Int, pcc	GM	Overstreet et al. 2009[19]
Pseudoacanthostomum panamense Caballero, Bravo-Hollis & Grocott, 1953	*Mugil curema*		EP	Pulido-Flores et al. 2015
Family: Cyathocotylidae				
Mesostephanus appendiculatoides (Price, 1934)	*Mugil curema*	int, stom, pcc	SE	Hutton 1964; Oren 1981
Family: Diplostomidae				
Austrodiplostomum mordax Szidat & Nani, 1951	Mugil curema	brn	EP	Pulido-Flores et al. 2015
Family: Fellodistomidae				

Tergestia laticollis (Rudolphi, 1819)	*Caranx hippos*	int	CS, SE, GM	Bunkley-Williams & Williams 1994
Family: Haploporidae				
Culuwiya beauforti (Hunter & Thomas, 1961) Overstreet & Curran, 2005	*Mugil curema*	int, pcc	GM, SA,SE	Bashirullah & Aguado 2009
Intromugil mugilicolus (Shireman, 1964) Overstreet & Curran, 2005	*Mugil curema*	int	GM	
Xiha fastigata (Thatcher & Sparks, 1958) Andres, Curran, Fayton, Pulis & Overstreet, 2015*	*Mugil curema*	int, pcc	GM, SA, SE, EP	Bashirullah & Aguado 2009[20]
Family: Haplosplanchnidae				
Haplosplanchnus mugilis Nahhas & Cable, 1964*	*Mugil curema*	int	CS, SE	Williams et al. 1996; Overstreet 1981
Hymenocotta manteri Manter, 1961*	*Mugil curema*	int	CS	Williams et al. 1996[21]
Schikhobalotrema acutum (Linton, 1910) Skrjabin & Guschanskaja, 1955	*Strongylura marina*	int	GM, SE, SA, EP	Overstreet et al. 2009
Schikhobalotrema elongatum Nahhas & Cable, 1964*	*Mugil curema*	int	CS	Dyer et al. 1998
Family: Hemiuridae				
Brachyphallus parvus (Manter, 1947)	*Caranx hippos*	sto	SE, NE, CS	Bunkley-Williams & Williams 1994
Ecternurus americanus (Manter, 1947)	*Caranx hippos*	sto		
Ectenurus lepidus Looss, 1907	*Caranx hippos*	sto, gil	SE, GM, SA, NE	Bunkley-Williams & Williams 1994
Ectenurus virgulus Looss, 1910	*Caranx hippos*	Int, sto	GM, SE, NE, CS	Overstreet et al. 2009
Ectenurus yamagutii Nahhas & Powell, 1971	*Caranx hippos*	sto	GM, SA	Overstreet et al. 2009
Lecithochirium floridense (Manter, 1934) Crowcroft, 1946*	*Sphyraena barracuda; Caranx hippos*	sto	CS, SE, GM	Saunders 1958; Ramso-Ascherl et al. 2015
Lecithochirium musculus (Looss, 1907) Nasir & Diaz, 1971	*Caranx hippos, Sphyraena barracuda*	Int, pcc, sto	GM, CA, EA, WP	Overstreet et al. 2009
Lecithocladium excisum (Rudolphi, 1819) Lühe, 1901	*Sphyraena barracuda*	sto	CS, SE	Bunkley-Williams & Williams 1994

Paradinurus manteri Vigueras, 1958	*Sphyraena barracuda*	sto	GM	Overstreet et al. 2009
Parahemiurus merus (Linton, 1910) Woolcock, 1935	*Caranx hippos, Sphyraena barracuda*	sto	GM, CS, SA, EP	Overstreet et al. 2009
Plerurus digitatus (Looss, 1899) Looss, 1907	*Sphyraena barracuda*	sto	WP, IO	Bray et al. 1993
Saturnis belizensis Fischthal, 1977	*Mugil curema*	sto	CS	Blasco-Coasta et al. 2006
Family:Heterophyidae				
Ascocotyle longa Ransom, 1920	*Mugil curema*	int, sto, pcc, liv, hrt, glb, spl, wvs	SE, SA, GM, CS	Martorelli et al. 2012[22]
Heterophyes heterophyes	*Mugil curema*	int, sto	ME, WP	Overstreet 1981
Family: Hirudinellidae				
Hirudinella ventricosa (Pallas, 1774) Baird, 1853	*Sphyraena barracuda*	sto	SE, SA, GM, SC, NE	Bunkley-Williams & Williams 1994
Family: Lecithasteridae				
Hysterolecitha rosea Linton, 1910	*Mugil curema*	int, sto	CS	Dyer et al. 1985
Lecithaster helodes Overstreet, 1973*	*Mugil curema*	Int, pcc	GM, SA	Overstreet et al. 2009
Family: Lepocreadiidae				
Neolepidapedoides belizensis (Fischthal, 1977) Bray & Gibson, 1989	*Sphyraena barracuda*	int	CS	Bunkley-Williams & Williams 1994[23]
Family: Monorchiidae				
Lasiotocus mugilis Overstreet, 1969*	*Mugil curema*	int	CS	Dyer et al. 1985
Family: Opecoelidae				
Pseudopecoeloides carangi (Yamaguti, 1938) Yamaguti, 1940	*Sphyraena barracuda, Caranx hippos*	int	SE	Bunkley-Williams & Williams 1994
Class: Monogenea				
Subclass: Monopisthocotylea				

Family: Ancyrocephalidae				
Ancyrocephalus cornutus Williams & Rodgers, 1972	*Strongylura marina*	gil	SE, IO	Williams & Rodger 1972[24]; Kristsky 2018[24]
Ancyrocephalus parvus Linton, 1940*	*Strongylura marina*	gil	SE, IO	Williams & Rodger 1972; Kristsky 2018
Ancyrocephalus tylosuri (MacCallum, 1917) Johnson & Tiegs, 1922	*Strongylura marina*	gil	IO	Kristsky 2018
Aristocleidus hastatus Mueller, 1936	*Gerres cinereus*	gil	GM	Franco et al. 2008
Ligophorus mugilinus(Hargis, 1955) Euzet & Suriano, 1977*	*Mugil curema*	gil	EP	Kohn et al. 2006[25], Fajer et al. 2005[26]
Family: Capsalidae				
Neobenedenia pacifica Bravo-Hollis, 1971	*Mugil curema*	ext	CS	Fajer et al. 2005
Family: Dionchidae				
Donchus remorae (MacCallum, 1916) Price, 1938	*Caranx hippos*	gil	CS	Kohn et al. 2006
Family: Diplectanidae				
Diplectanum collinsi (Müller, 1936) Price, 1937*	*Gerres cinereus*	gil	CS	Kohn et a. 2006
Neodiplectanum wenningeri Mizelle & Blatz, 1941	*Gerres cinereus*	gil	SE	Dominques et al. 2011
Pseudolamellodiscus sphyraenae Yamaguti, 1953	*Sphyraena barracuda*	gil	IO	Al-Zubaidy 2013
Family: Gyrodactylididae				
Gyrodactylus curemae Conroy & Conroy, 1985*	*Mugil curema*	gil	GM	Saldgao-Maldonado & Aldrete 2000
Subclass: Polypisthocotylea				
Family: Allopyragraphoridae				
Allopyragraphorus caballeroi (Zerecero, 1960) Yamaguti, 1963	*Caranx hippos*	gil	CS, GM	Boada et al. 2012; Kohn et al. 2006
Allopyragraphorus hippos (Hargis, 1956) Yamaguti, 1963*	*Caranx hippos*	gil	GM, SE, CS	Boada et al. 2012; Kohn et al. 2006; Kristsky et al. 2011
Allopyragraphorus incomparabilis Yamaguti, 1963	*Caranx hippos*	gil	CS, GM	Boada et al. 2012; Kohn et al. 2006

Allopyragraphorus marinae Zambrano, 1998	*Strongylura marina*	gil	GM, SA	Fuentes Zambrano 1998
Allopyragraphorus winteri (Caballero & Bravo-Hollis, 1965) Bravo-Hollis & Salgado-Maldonado, 1983	*Caranx hippos*	gil	GM	Kohn et al. 2006
Family: Cemocotylidae				
Cemocotyle carangis (MacCallum, 1919) Sproston, 1946*	*Caranx hippos*	gil	CS	Kohn et al. 2006
Cemocotyle noveboracensis (MacCallum, 1919) Price, 1962*	*Caranx hippos*	gil	GM, CS, SE	Boada et al. 2012; Kristsky et al. 2011; Kohn et al. 2006
Cemocotylella elongata (Meserve, 1983) Price, 1962	*Caranx hippos*	gil	CS	Bunkley-Williams & Williams 1994
Family: Chauhaneidae				
Ahpua piscicola Caballero & Bravo-Hollis, 1973	*Caranx hippos*	gil	GM	Kohn et al. 2006
Cotyloatlantica pretiosa Bravo-Hollis, 1984	*Sphyraena barracuda*	mou, gil	GM	Kohn et al. 2006
Pentatres sphyraenae Euzet & Razarihelisoa, 1959	*Sphyraena barracuda*	gil	IO	Al-Zubaidy 2013
Pseudochauhanea mexicana Lamothe, 1967	*Sphyraena barracuda*	gil	GM	Kohn et al. 2006
Pseudochauhanea sphyraenae Yamaguti, 1965*	*Sphyraena barracuda*	gil	SE	Skinner 1978
Pseudomazocraes monsivaise Caballero & Bravo-Hollis, 1955	*Caranx hippos*	gil	GM	Kohn et al. 2006
Pseudomazocraes riojai (Caballero & Bravo-Hollis, 1963) Lebedev, 1970	*Caranx hippos*	gil	GM	Kohn et al. 2006
Pseudomaxocraes selene Hargis, 1957	*Caranx hippos*	gil	GM	Kohn et al. 2006
Family: Heteraxinidae				
Zeuxapta seriolae (Meserve, 1938)	*Caranx hippos*	gil	GM	Kohn et al. 2006[25]
Family: Mazocraeidae				
Salinacotyle mexicana (Caballero & Bravo-Hollis, 1963) Lebedev, 1984	*Caranx hippos*	gil	GM	Kohn et al. 2006
Family: Microcotylidae				
Metamicrocotyla chamelensis Bravo-Hollis, 1983	*Mugil curema*	gil	GM	Kohn et al. 2006

Metamicrocotyla macrantha (Alexander, 1954) Koratha, 1955*	*Mugil curema*	gil	CS, SE	Kohn et al. 2006; Skinner 1978
Metamicrocotyla pacifica Bravo-Hollis, 1982	*Mugil curema*	gil	GM	Kohn et al. 2006
Microcotyle neozealanicus Dillon & Hargis, 1965	*Gerres cinereus*	gil	CM	Kohn et al. 2006
Rhinecotyle deloyai Bravo-Hollis, 1981	*Sphyraena barracuda*	gil	GM	Laffon-Leal 2007
Solostamenides pseudomugilis (Hargis, 1956)	*Mugil curema*	gil	GM	Kohn et al. 2006
Family: Protomicrocotylidae				
Neomicrocotyle pacifica (Meserve, 1938) Yamaguti, 1968	*Caranx hippos*	gil	CS, GM	Kohn et al. 2006
Protomicrocotyle manteri Bravo-Hollis, 1966	*Caranx hippos*	gil	GM	Kohn et al. 2006
Protomicrocotyle mirabilis (MacCallum, 1918) Johnson & Tiegs, 1922*	*Caranx hippos*	gil	EP, SE	Boada et al. 2012; Kristsky et al. 2011
Vallisiopsis contorta Subhapradha, 1951	*Sphyraena barracuda*	gil	IO	Al-Zubaidy 2013

[1] Reported as the junior synonym *Holobolochus crevalleus*
[2] Reported as the junior synonym *Ergasilus nanus*
[3] Occurs in the larval form
[4] Occurs in the blastocyst stage
[5] Occurs in the post-larval stage
[6] Occurs in the encapsulated larval stage
[7] Unaccepted larval name. Family Tetraphyllidea incerte sedis
[8] Reported as the junior synonym *Dihenistephanus brachyderus*
[9] Reported as the junior synonym *Stephanostomum longosimum*
[10] Reported as the junior synonym *Monochistephanostomum gracile*
[11] Reported as the junior synonym *Bucephalus introversus*
[12] Reported as the junior synonym *Bucephalus varicus*
[13] Reported as the junior synonym *Bucephalus carangoides*
[14] Reported as the junior synonym *Bucephaloides longicirrus*
[15] Possible false host
[16] Reported as the junior synonym *Bucephaloides arcuatus*
[17] Reported as the junior synonym *Bucephalopsis attenuata*
[18] Reported as the junior synonym *Bucephalopsis gracilescens*

[19] Possible false host
[20] Reported as the junior synonym *Dicrogaster fastigata*
[21] Reported as junior synonym *Hymenocottoides manteri*
[22] Reported as junior synonym *Ascocotyle (Phagicola) longa*
[23] Possible false host
[24] incertae sedis
[25] Reported as junior synonym *Pseudohaliotrema mugilinus*
[26] Reported as junior synonym *Haliotrema mugilinus*

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Appendix 2: Descriptions of Identified Parasite Species

Monogenea

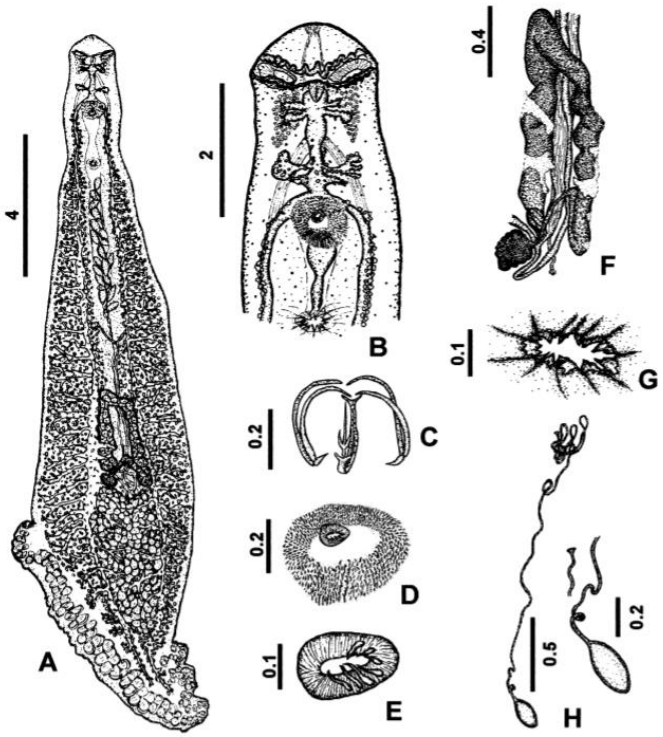
Allencotyla mcintoshi Price, 1962

Description: Elongated worm, body lanceolate. Tegument smooth. Haptor 978.91 ɯm. Clamps asymmetrical. Clamps on long side larger and more numerous than those on the shorter side. 30-40 clamps on long size and 10-15 clamps on the short side. Largest clamps 58 ɯm x 59 ɯm and the smallest 34 ɯm x 45 ɯm The larger clamps occur medially. Vitellaria extends throughout body. Two subelliptical sucker present anteriorly with subtriangular are of glandular cells behind each sucker. Vagina present, unarmed, with pointed folds. Genital atrium armed with 8 concentric rows of numerous spines (300-400).

Host: *C. hippos*

Location: Gill filaments

Taxonomic/Image Reference: Montero et al. 2003. Page 133. Figure 1. Size measures in centimeters.



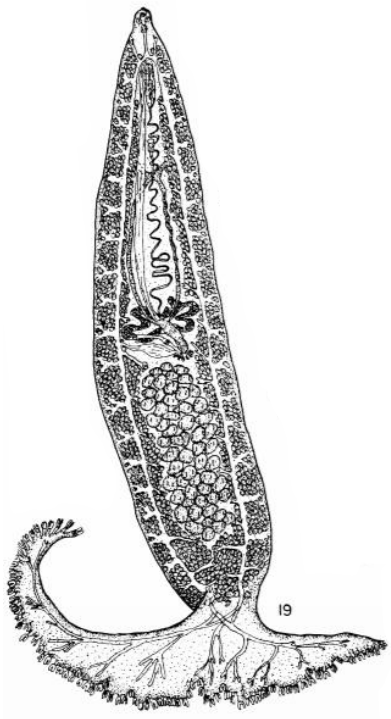
Allopyragraphorus hippos (Hargis, 1956) Yamaguti, 1963

Description: Body broad. Haptor on peduncle from body proper. Haptor almost same length and shape of body. Clamps numerous 50-60 on the ventral lip of haptor. Clamps ovoid in shape and present on stalks extending away from haptor. Size similar across all clamps 46 ɯm x 64 ɯm .One pair of ovoid buccal suckers present anteriorly of pharynx. Denticle like papillae present on the edge of sucker. Pharnyx circular to ovoid. Gut bifurcation occurs directly posterior to genital aperture. Genital atrium and cirrus unarmed. Vagina dorsal and directly posterior to genital aperture. Vitellaria dense extending from directly posterior of the pharynx to the base of the opistohaptor. Vein-like projections of vitellaria extend into the opistohaptor.

Host: *C. hippos*

Location: Gill Filaments

Taxonomic/Image Reference: Hargis 1956. Page 447. Figures 19-20. Identified as synonymized name *Pyragraphorus hippos.*



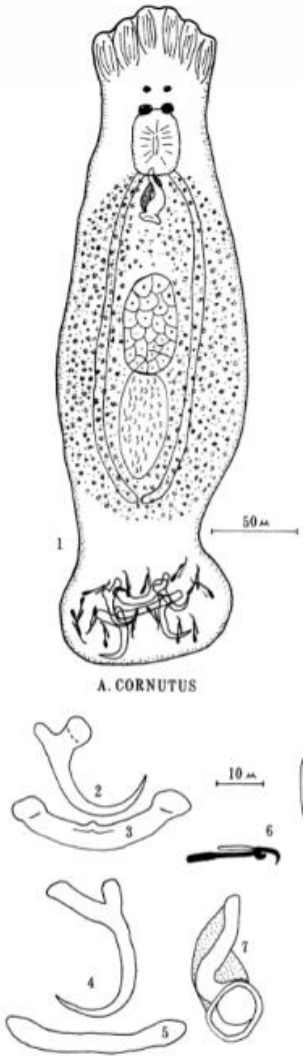
Ancryocephalus cornutus

Description: Small, robust worm. Anterior area fan shaped with 6 elongate head organs. Two pairs of eyespots located posterior of head organs with the posterior pair twice as large as the anterior pair. Gut bifurcated. Haptor truncated. Ventral and dorsal hooks similar in size and shape. Anchor with long root and small superficial root. Two transverse bars present. Ventral bar straight with slightly expanded ends. The dorsal bar curved in mid-region and expanded ends. 14 sickle shaped accessory hooks present on haptor. Horn shape cirrus directly posteriorly. Accessory piece long and curve with posterior end hooked shaped. Vitellaria dense. This species is considered

Host: *S. marina*

Location: Gill Filaments

Taxonomic/Image Reference: Williams & Rodgers 1972. Page 877, Figures 1-7



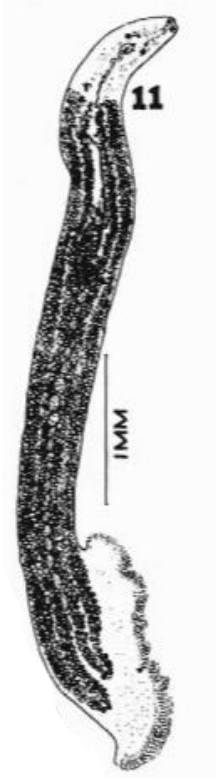
Axinoides gracilis (Linton, 1940)

Description: Body elongate. Prohaptoral suckers oval with denticle like papillae around opening. Haptor wing like with a single row of 42-82 clamps on the margin. Haptor anchors present axinid in shape. Pharnyx present and oval in shape. Gut bifurcated slightly anterior of genital aperture. Genital atrium unarmed but transverse ridges are present. Cirrus present and unarmed. Testes ovoid and numerous, postovarial. Ovary J-shapes and in the anterior in the anterior third of body. Vagina dorsal and located directly posterior to genital aperture. Vitellaria extending from slightly distal to vaginal aperture.

Host: *S. marina*

Location: Gill Filaments

Taxonomic/Image Reference: Price 1962A. Page 7. Figure 11. Identified synonymized name *Nudaciraxine gracilis*.



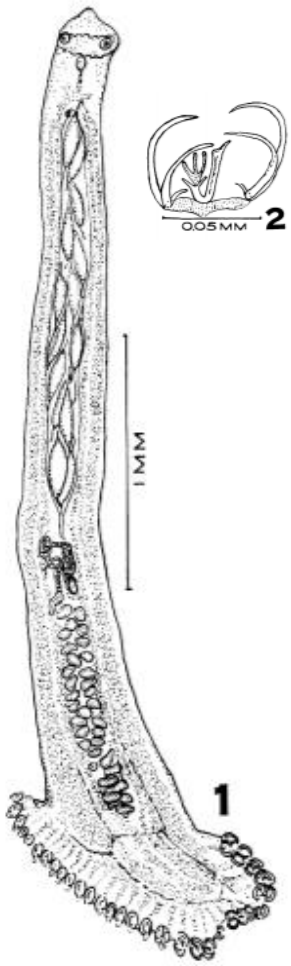
Cemocotylella elongate (Meserve, 1938)

Description: Minuscule elongated worm. Haptor oval shaped with a break in clamp assemblage at the most posterior end. Haptor asymmetrical. 23-25 clamps on long end and 4-6 clamps on short side. Vagina absent. Genital atrium lacking spines. Eggs numerous and ovoid shaped. Associated in the east Caribbean Sea with *A. hippos* and *C. noveboracensis.*

Host: *Caranx hippos*

Location: Gill filaments

Taxonomic/Image Reference: Price 1962B. Page 410. Figures 1-2



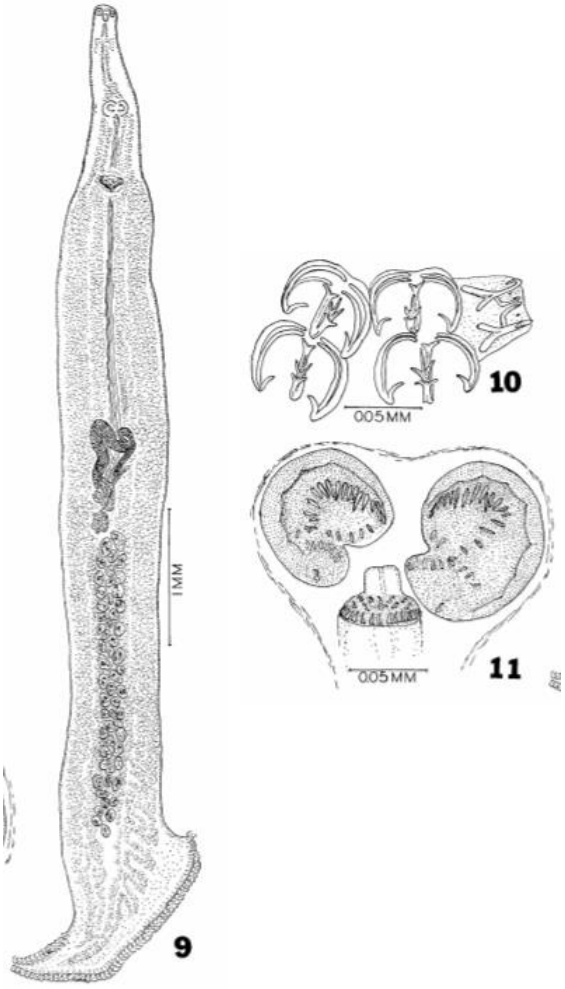
Cemocotyle noveboracensis (MacCallum, 1919) Price, 1962

Description: Elongated relatively thin worm. Haptor with pointed tip that curves away from remainder of body. Clamps circular and similar in shape and size throughout haptor. Clamps extend to both sides of haptor asymmetrically. Sinstral side of haptor containing 43-45 clamps and dextral side containing 15-17 clamps. Mouth at anterior end of body. Pharynx directly anterior to genital opening. Genital atrium contains lateral muscular pockets. Muscular pockets cuplike and armed with hook-like spines. Cirrus muscular, armed with 3-4 rows of hook like spines. This species is genus specific to *Caranx* and found regularly in *C. hippos*.

Host: *C. hippos*

Location: Gill Filaments

Image Reference: Price 1962B. Page 406 Figures 9-11.



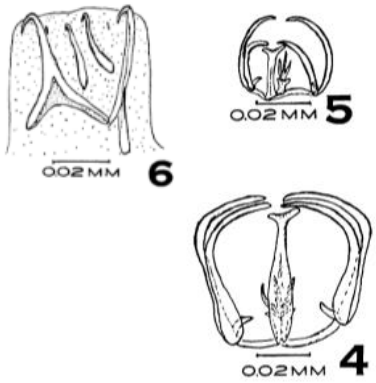
Cemocotyle saquae Manter & Prince, 1953

Description: Elongated slim worm. Similar morphologically to *C. noveboracensis.* Haptor with pointed tip in line with body center. Clamps asymmetrical. Longer side of opistohaptor containing 20-22 smaller heart shaped clamps. Short side containing 5-7 larger rectangle shaped clamps. Two pairs of anchor hooks present at tip of opistohaptor. One pair with distended basal structures and on pair with slim basal structures. Mouth at anterior end of body. Vagina absent. Genital atrium lacking spines.

Host: *C. hippos*

Location: Gill Filaments

Taxonomic/Image Reference: Price 1962B Page 410. Figures 4-6.



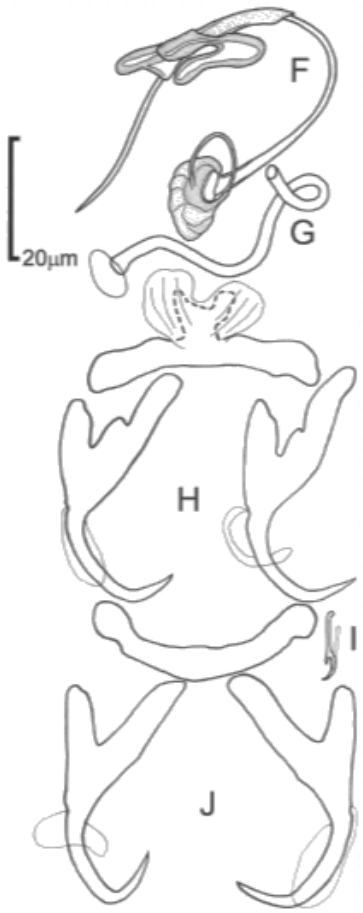
Ligophorus mugilinus (Hargis, 1955) Euzet & Suriano, 1977

Description: Elongated worm. Tegument smooth. 2 pairs of anchors present. Similar in size and shape. Base noticeably thicker than blade. Base and blade separated by notch. Each set of anchors connected by transverse bars. Transverse bars distinctly different. Ventral transverse bar massive with heavily sclerotized median process flanked by 2 membranous anterior processes. Dorsal transverse bar V-shaped with curved ovate terminal ends. Vitellaria bifurcated and contained to mid body. Penis tubular with claw-shaped accessory piece.

Host: *M. curema*

Location: Gill Filament

Taxonomic/Image Reference: Sarabeev et al. 2005. Page 1447. Figures F-J



Metamicrocotyla macracantha (Alexander, 1954) Koratha, 1955

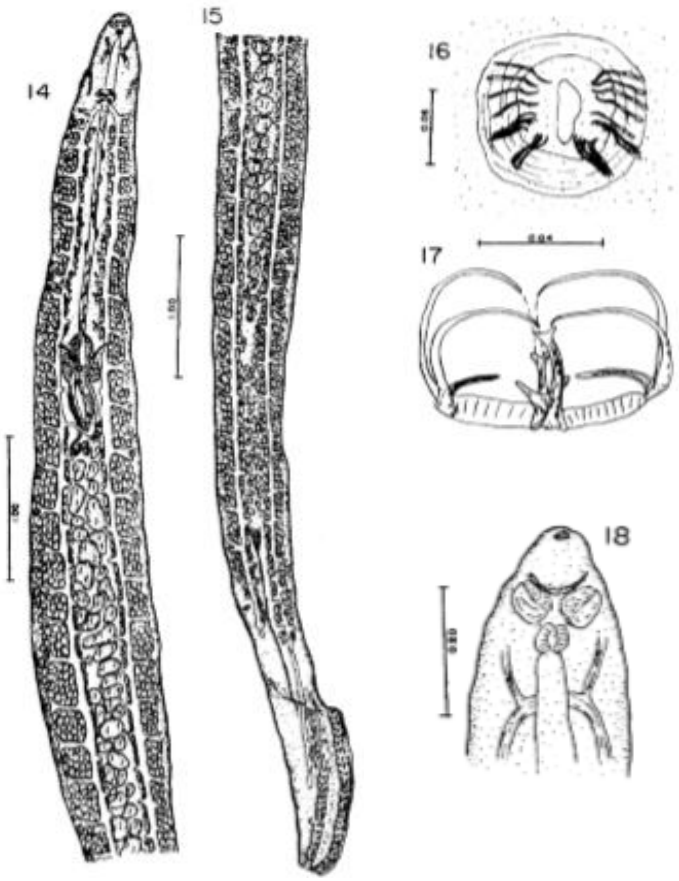
Description: Body long and slender. Vitellaria dense extending from level of genital atrium to pseudosucker. Pseudosucker present anteriorly of haptor. Buccal suckers present and elliptical Pharnyx globular. Genital atrium present with 13-17 spines on each side. Testes follicular and ovary tubular. Haptor present posteriorly and peduncle from body proper. Clamps in two asymmetrical rows. 30-60 clamps per row. Clamps microcotylid type and similar in shape but variable in size with the largest clamps occurring in the middle.

Host: *M. curema*

Location: Gill Filaments

Taxonomic Reference: Kohn et al. 1994. Page 128.

Image Reference: Hargis 1956. Page 447. Figures 14-18.



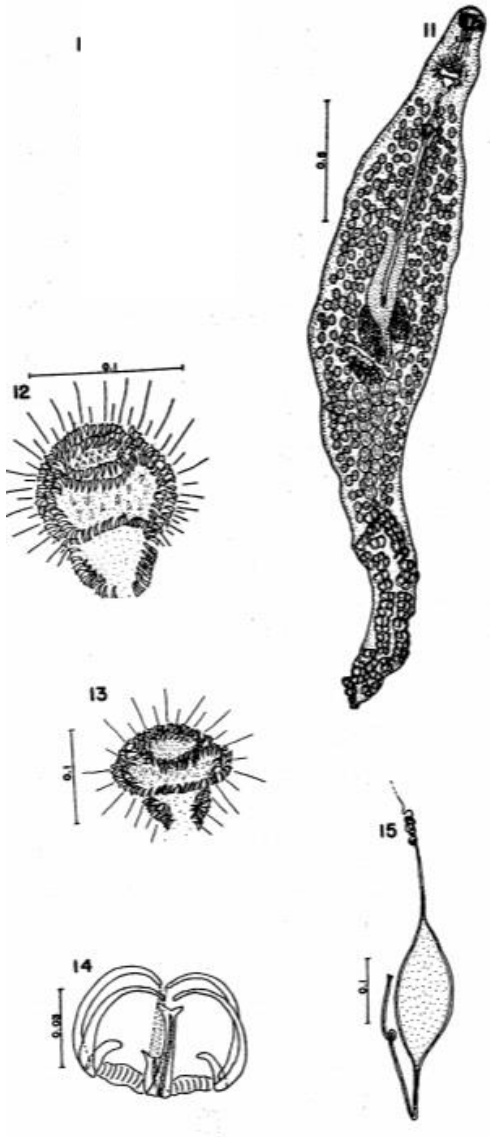
Microcotyle neozealanicus Dillon & Hargis, 1965

Description: Body elongate. Pair of buccal sucker present, elliptical in shape, with papillae on rims. Gut bifurcation occurring directly behind genital atrium. Haptor present with two symmetrical rows with 28 pairs each. Clamps similar in shape, micocotylid type, but dissimilar in size. The largest clamps present in the middle and the smallest clamps present posteriorly. Pharynx present. Testes postovarian. Cirrus present bulbous in shape and unarmed. Genital atrium armed with numerous spines, Ovary tubular. Vagina present. Vitellaria dense. Extending from the level of gut bifurcation to anterior portion of haptor.

Host: *G. cinereus*

Location: Gills

Reference: Dillon et al. 1985 Page 8-9. Plate II, Figures 11-15.



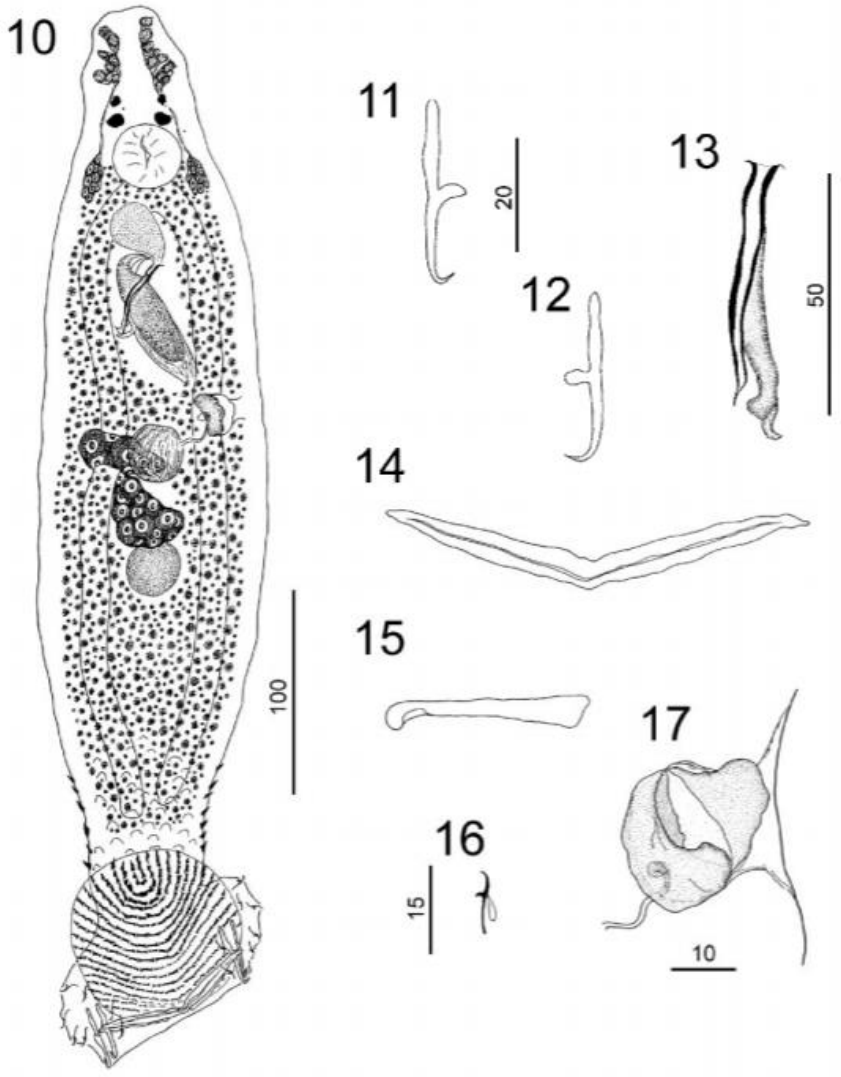
Neodiplectanum mexicana (Mendoza Franco, Roche & Torchin, 2008)

Description: Body elongate, broad posteriorly. Tegument scaled. Head organs arranged in four groups each associated with cephalic lobe. Four eye spots, more anterior pair smaller. Pharynx directly posterior to eye spots, sub-spherical. Peduncle broad. Haptor located at posterior end of body. Squamodisc present, dorsal and ventral on haptor, formed by 20 rings of concentric sclerites. Four anchors present with straight roots, connected by one transverse bar with bend at middle. Anchors similar in shape and size. Accessory hooks present on dextral and sinistral sides of haptor. Testis spherical. Accessory piece elongate with hook shaped tip. Vitellaria small follicles, located densely throughout body proper extending anteriorly to level of pharynx.

Host: *G. cinereus*

Location: Gills

Taxonomic/Image Reference: Mendoza Franco et al. 2008. Pages 174-175. Figures 10-17. Measurements in ɯm.



Neodiplectanum wenningeri Mizelle & Blatz, 1941

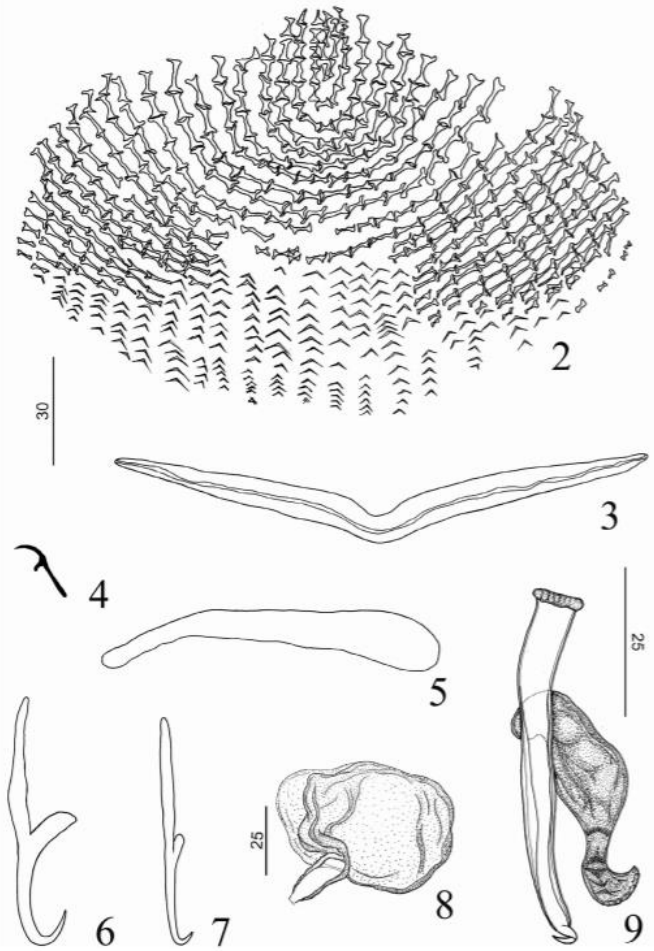
Description: Small, elongate worm. Four eye spots present with the larger pair found posteriorly. Pharnyx present and circular in shape. Vitellaria dense and extending into anterior portion of peduncle. Haptor disc-like with squamodiscs connected to the body proper by a peduncle. Squadiscs composed of twenty-five to thirty concentric rows of cuticular structures. Two transverse bars present. Both dissimilar in size and shape, but bent posteriorly down the middle. Dorsal bar with knobbed ends and ventral bar with pointed ends. Anchors similar in shape, slender with bifurcated bases. Anchors have deep roots. Six pairs of accessory hooks present with sickle shapes termination. Vagina present and located in posterior half of body

Host: *G. cinereus*

Location: Gill Filaments

Reference: Mizelle & Blatz 1941. Page 107-108.

Image Reference: Domingues et al. 2011. Page 5, Figures 2-9



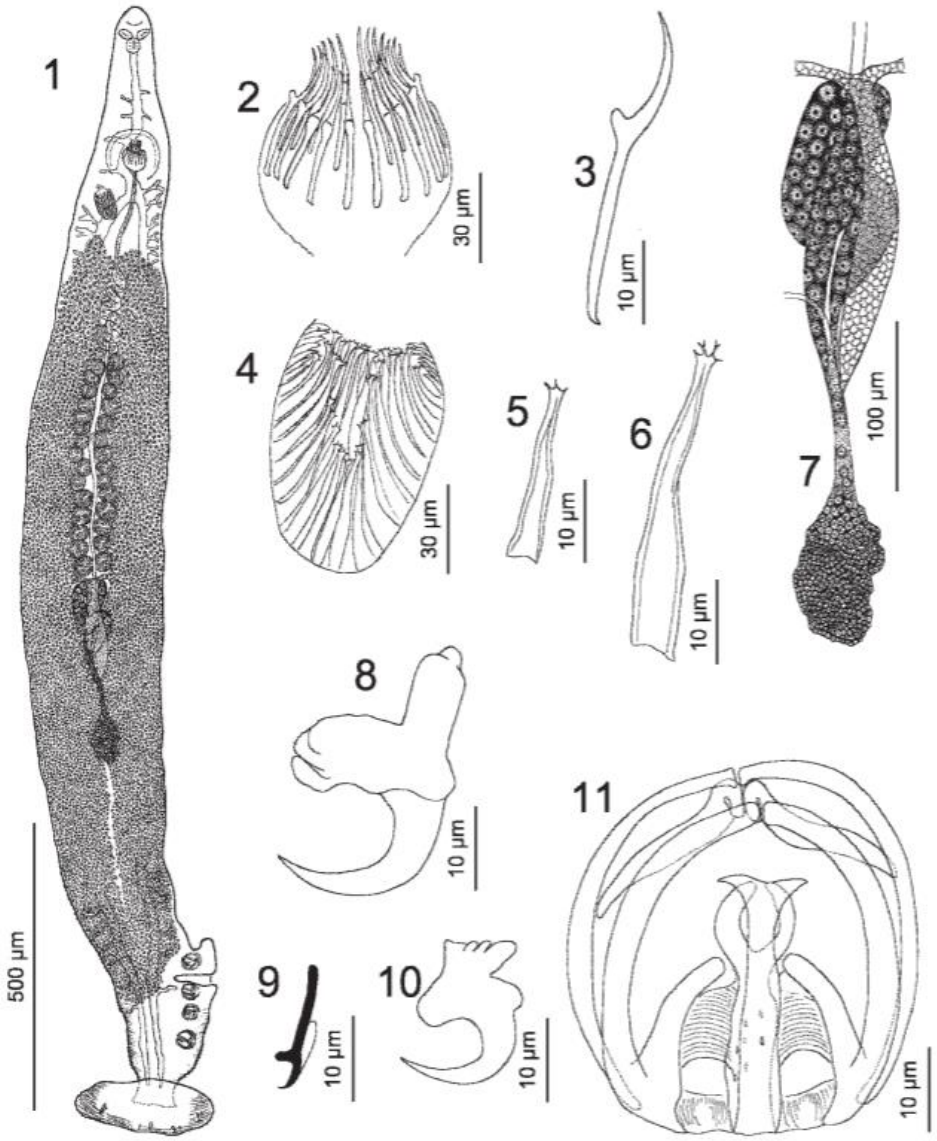
Protomicrocotyle mirabilis (MacCallum, 1918) Johnstpn & Tiegs, 1922

Description: Long elongate worm. Haptor asymmetrical. Four unilateral sessile clapms present. Large terminal lappet distally originating from haptoral constriction. Lappet transversely elongated ovate. Three pairs of ventral sclerites present; 1 pair of hooks and 2 pairs of anchors. Genital atrium unarmed. Male copulatory organ armed with 19 tight concentric spines that extend to level of genital atrium. Vagina present armed with numerous flattened spines.

Host: *C. hippos*

Location: Gill Filaments

Taxonomic/Image Reference: Kristsky et al. 2011. Page 267. Figures 1-11.



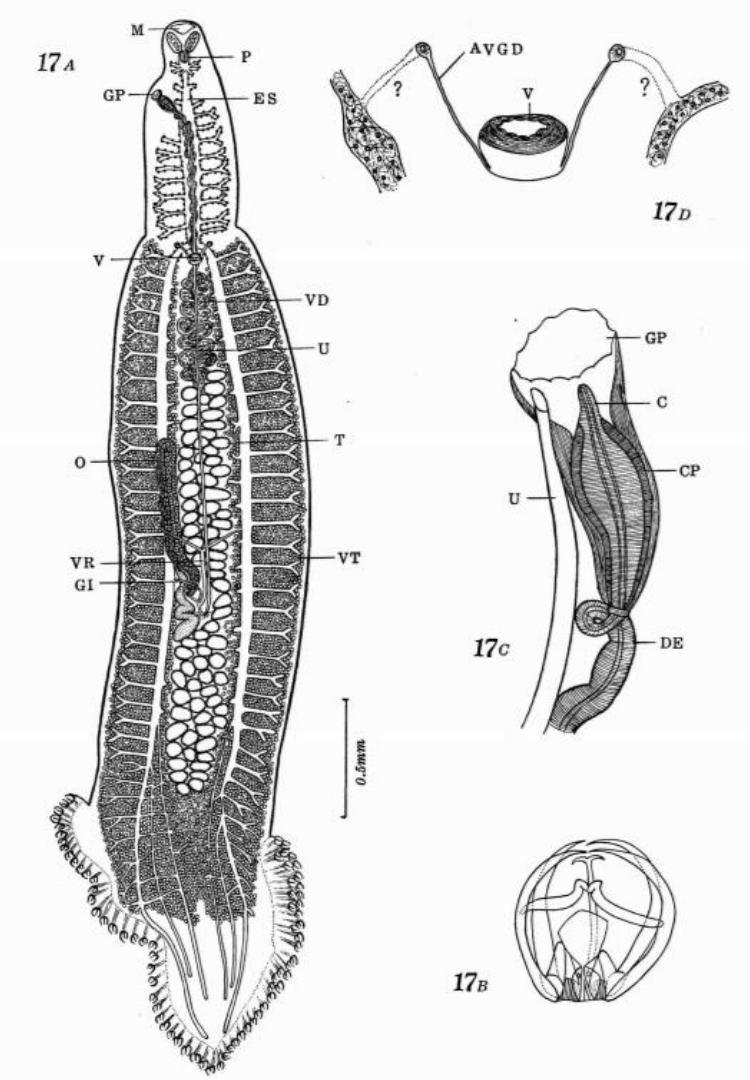
Pseudochauhanea sphyraenae Yamaguti, 1965

Description: Lanceolate body. Anterior end of body narrow with body becoming abruptly wider at level of vagina. Haptor v-shaped with two asymmetrical rows of spines. 30-50 clamps on longer side and 25-35 clamps on shorter side. Opistohaptor without terminal anchors. Head rounded. Pair of buccal sucker elliptical. Pharynx globular, small, directly posterior to buccal suckers. Genital pore dextral posterior to pharynx. Intestinal branches protruding laterally anteriorly of vagina. Cirrus unarmed opening into wide genital atrium. Ovary irregular, contained to the dextral side of midbody. Vitellaria dense throughout body proper to level of anterior truncation.

Host: *S. barracuda*

Location: Gill Filaments

Taxonomic/Image Reference: Yamaguti 1965. Page 90, Figure 17A-17D



Digenea

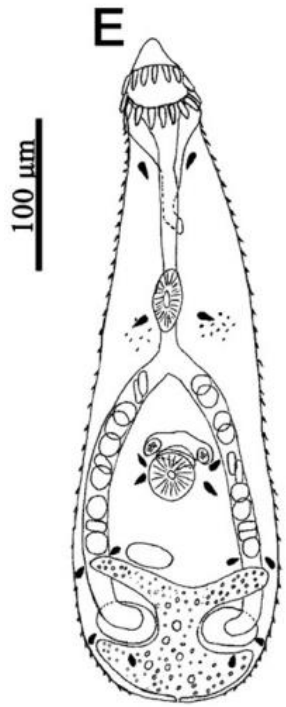
Ascocotyle (*Phagicola*) sp. metacercariae

Description: Encysted metacercariae, numerous. Cyst oval, thin-walled, translucent. Popped cysts produced pyriform metacercariae. Body tegument spinous. Single row of 14-17 circumoral spines present around oral sucker. Pre-oral lobe triangular. Pharynx present, well developed, located in the midbody directly anterior to the level of gut bifurcations. Reproductive structures were not developed enough to be distinguished. Based on previous described ascocotyle species in these fishes and distinguishable features this parasite could be *Ascocotyle longa* Ransom, 1920, but further phylogeny and molecular work would need to be done to validate it. A diagram of *A. longa* metacercariae is provided below as a reference.

Host: *G. cinereus* & *M. curema*

Location: Gills, Spleen, Heart, Liver, Gonads, Gall Bladder & Intestines

Taxonomic/Image Reference: Simões et al. 2010, Page 228, Figure E.



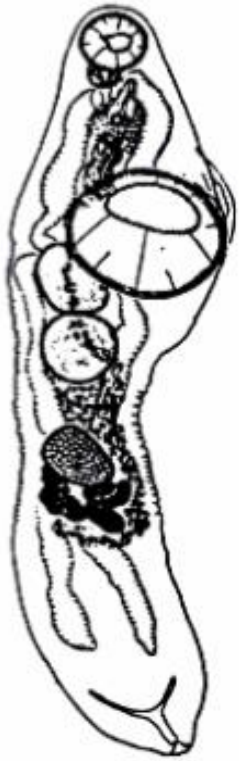
Brachyphallus parvus (Manter, 1947)

Description: Body small, elongate. Body surface smooth. Presomatic pit present. Pharnyx well developed. Oral and ventral sucker present, moderately separated, size ratio 1:2.5. Short tail present, usually withdrawn into body. Testes two, ovoid, opposite or tandem, overlapping posterior margin of ventral sucker. Seminal vesicle present mostly anterior of ventral sucker. Cirrus sac small and weakly developed. Ovary small, subspherical, directly anterior of vitellaria. Vitellaria two lateral masses, irregularly lobed, located in mid-hind body. This species was found in the stomach by Williams & Williams () but specimens in M. curema in this study were found in the gill filaments. This may be due to regurgitation of the stomach contents causing the parasites to get caught in the gill filaments.

Host: *M. curema*

Location: Gills

Taxononic/ Image Reference: Williams & Bunkley-Williams 1996. Page 30.



Metacercariae sp.

Description: Encysted digenea metacercariae. Cysts oval, thin-walled, translucent. Popped cysted produced fusiform metacercariae. Body tegument spinous or smooth. Oral and ventral sucker present, similar in size. Ventral sucker located at level of mid-body. Reproductive structures were not developed enough to be distinguishable. Lack of distinguishing features did not allow for further identification.

Host: *G. cinereus*

Location: Fins

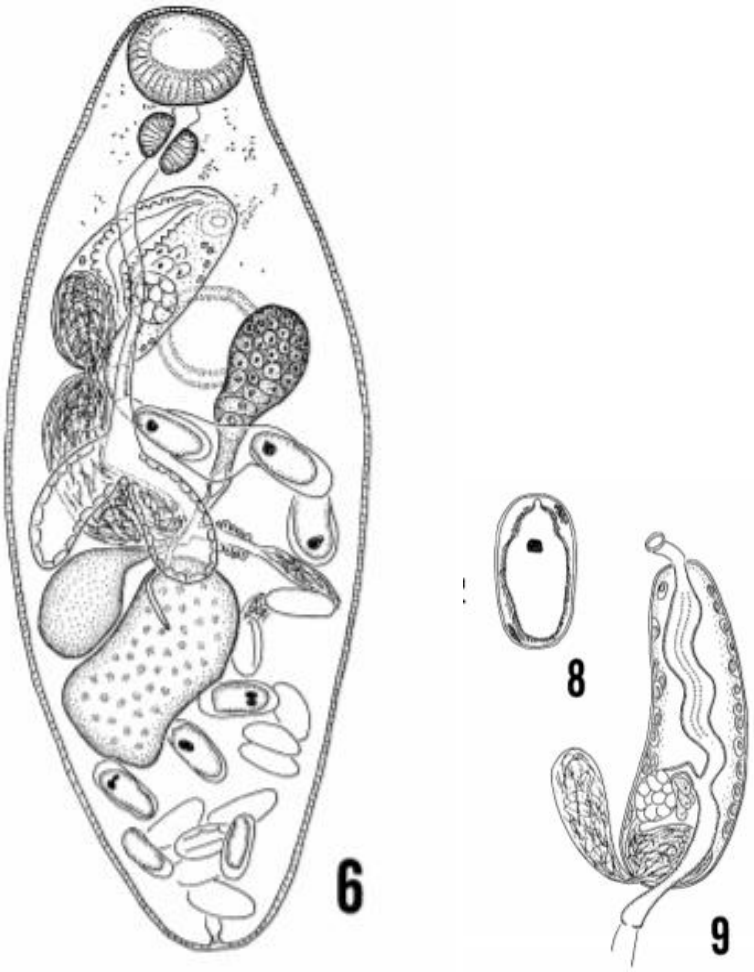
Xihu fastigata (Thatcher & Sparks, 1958) Andres, Curran, Fayton, Pulis & Overstreet, 2015

Description: Body small, fusiform. Oral and ventral sucker present similar in size 1:1.3. Ventral sucker small when compared to the body size. Pharynx well developed. Forebody short, 20% of body. Hermaphroditic sac present, elongate. Testes elongate, irregular, in the hindbody. Gential pore median, overlapping anterior margins of ventral sucker. Ovary pretesticular. Vitellaria contained to a distinct mass of follicles that is larger than the pharynx. Eggs large, numerous, miracidium with large eye-spot. Thatcher & Sparks (1958) placed this species in the genus *Dicrogaster*. These species was later synonymized with the current name *Xihu fastigata* by Anders et al. (2015)

Host: *M. curema*

Location: Stomach

Taxonomic/Image Reference: Overstreet 1971. Page 968, Figure 6-8. Described as synonymized name *Dicrogaster fastigata*



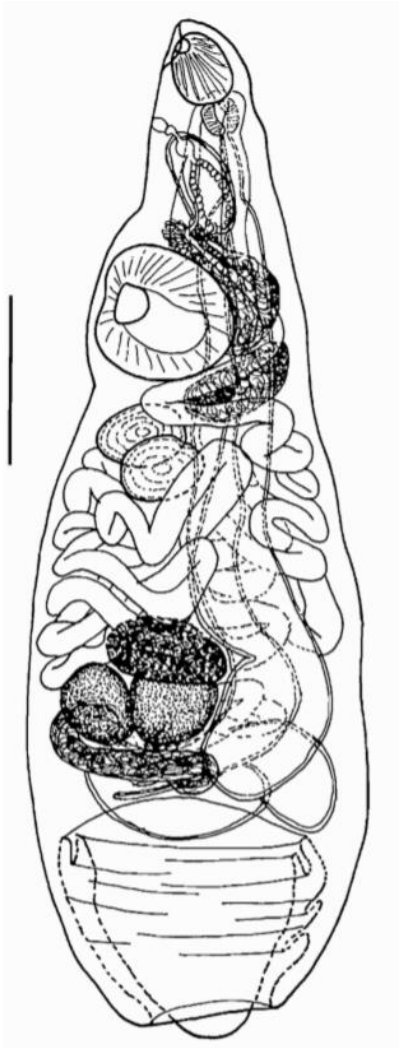
Dissosaccus laevis (Linton, 1898)

Description: Body elongate. Ecsoma well developed. Body surface smooth. Oral and ventral sucker present, moderately separated. Size ratio 1.23. Pharynx well developed, directly posterior to oral sucker Genital pore median at level of pharynx. Seminal vesicle present in two parts separated by narrow duct at level of ventral sucker. Testes two, ovoid, tandem. Ovary ovoid, in mid-body. Vitellaria two slightly indented masses with overlapping ventral margins with ovary..

Host: *M. curema*

Location: Stomach

Taxonomic/Image Reference: Margolis & Kabata 1996. Page 107, Figure 46



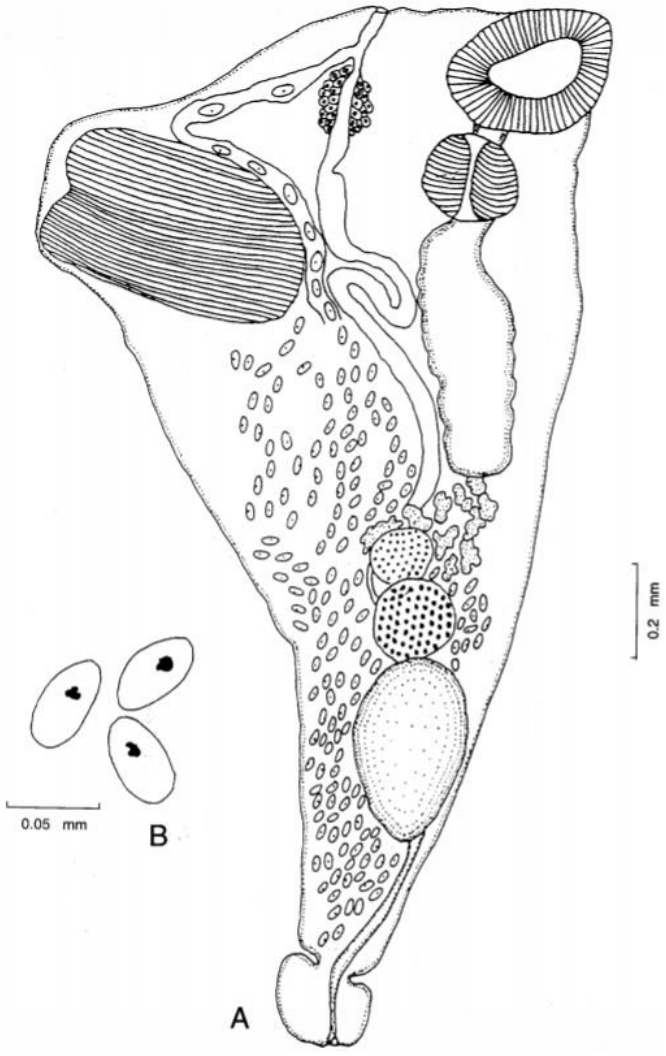
Haplosplanchnus mugilis Nahhas & Cable, 1964

Description: Body elongate aspinose. Oral and ventral sucker present. Oral sucker subspherical. Ventral sucker cup shaped. Pharynx well developed. Cecum simple ending blindly in anterior body. Genital pore median in between oral and ventral sucker. Testes one. Cirrus sac absent. Ovary pretesticular. Vitellaria subspherical to ovoid, located in between testes and ventral sucker. Eggs small, numerous, in mid and hindbody, miricidium with eye spots.

Host: *M. curema*

Location: Intestines

Taxonomic/Image Reference: Al-Bassel 1997. Page 136, Figure 2.



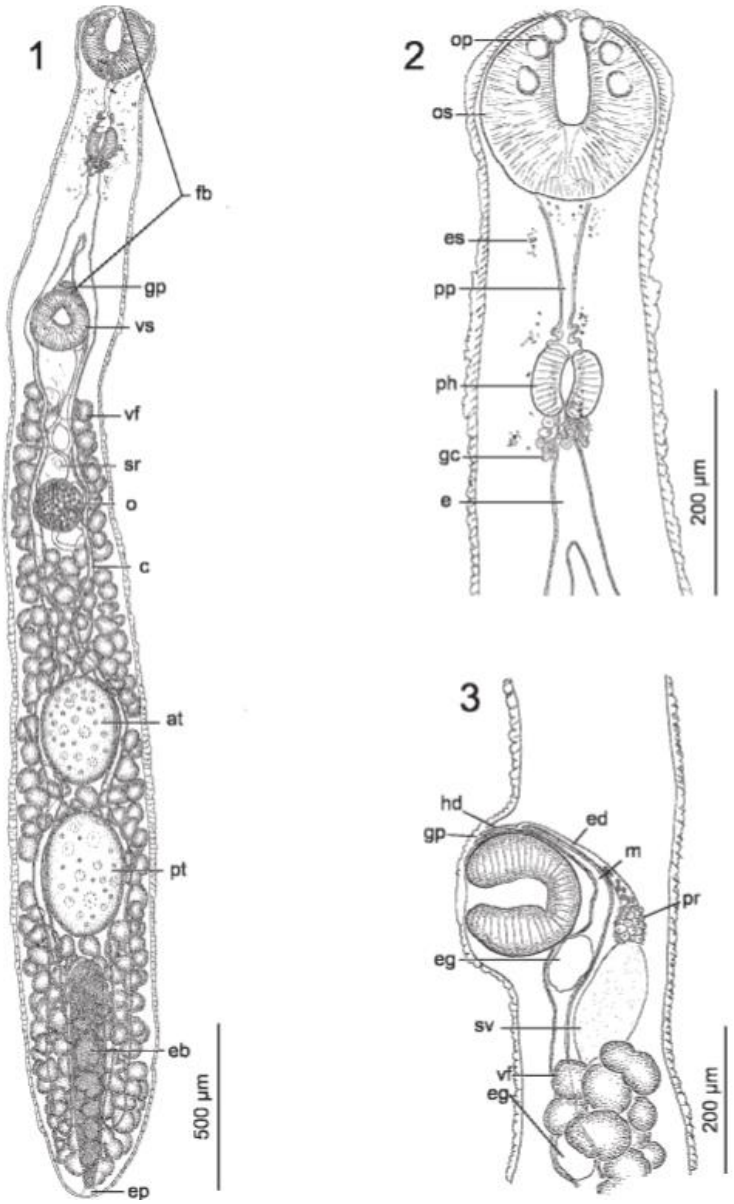
Homalometron elongatum Manter, 1947

Description: Body elongate. Tegument covered in small spines. Oral sucker and ventral sucker present. Oral sucker with three pairs of large papillae surrounding mouth opening. Sucker size ration 1:0.8. Pharynx well developed. Prepharynx elongated. Genital pore median, overlapping anterior margin with ventral sucker. Testes two, ovoid, tandem, in mid-hind body. Cirrus sac absent. Ovary spherical, pretesticular, in midbody. Vitellaria follicular in hind body. Eggs numerous, throughout mid and hindbody.

Host: *G. cinereus*

Location: Gills

Taxonomic/Image Reference: Parker et al. 2010. Page 157. Figure 1-3



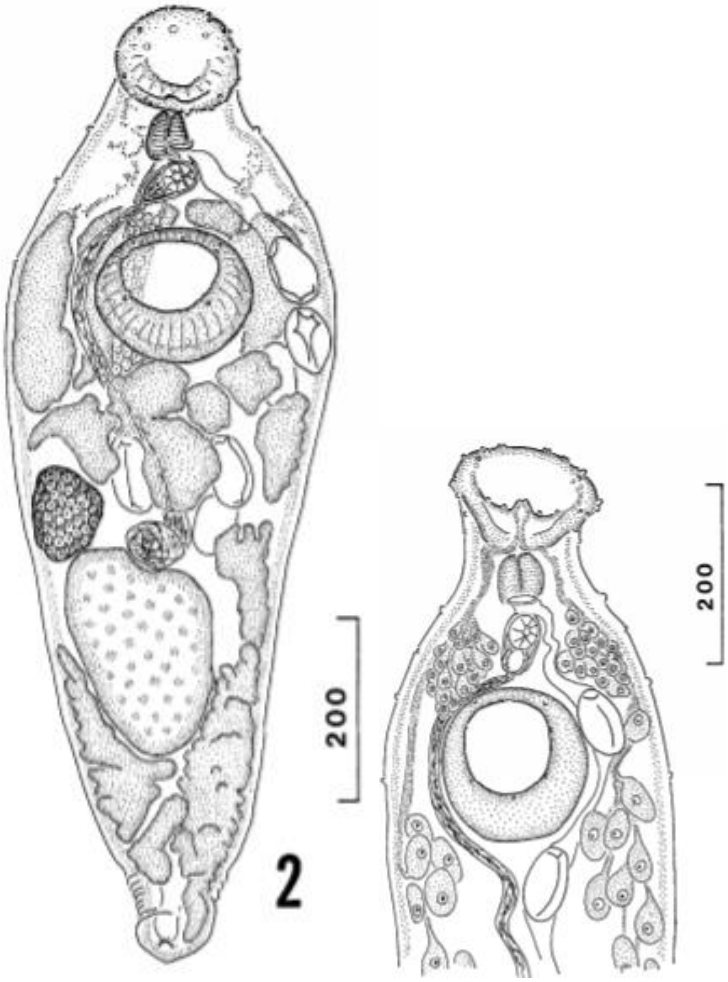
Hymenocotta manteri Overstreet, 1969

Description: Body elongate, fusiform. Tegument with papillae. Oral and ventral sucker present, moderately separated. Sucker size ratio 1:1.2. Oral sucker disc shaped, not lobed, can be compressed or expanded. Pharynx well developed. Prepharynx short. Genital pore median in between oral and ventral sucker. Cirrus sac present, but hard to distinguish. Testis one, irregular, in mid-body. Ovary subspherical, pretesticular. Vitellaria irregularly lobed extending from the level of ventral sucker to hind body. Eggs large, numerous in mid-body.

Host: *M. curema*

Location: Intestines & Stomach

Taxonomic/Image Reference: Overstreet 1971. Page 968. Figure 2-5.



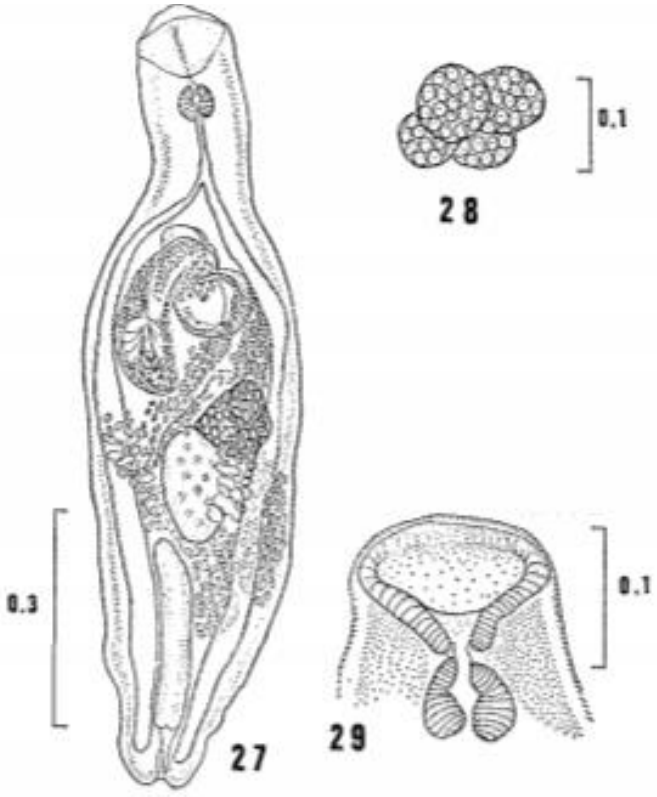
Lasiotocus mugilis Overstreet, 1969

Description: Body small, elongate. Forebody narrow. Tegument spinous. Oral and ventral sucker present similar in size. Oral sucker weakly developed, funnel-shaped. Ventral sucker small. Acetabulum weakly developed. Pharynx well developed. Prepharynx short. Testis one, subspherical. Ovary four lobed, pretesticular. Vitellaria contained in compact groups.

Host: *M. curema*

Location: Intestines

Taxonomic/Image Reference: Overstreet 1969. Page 153, Figure 27-29.



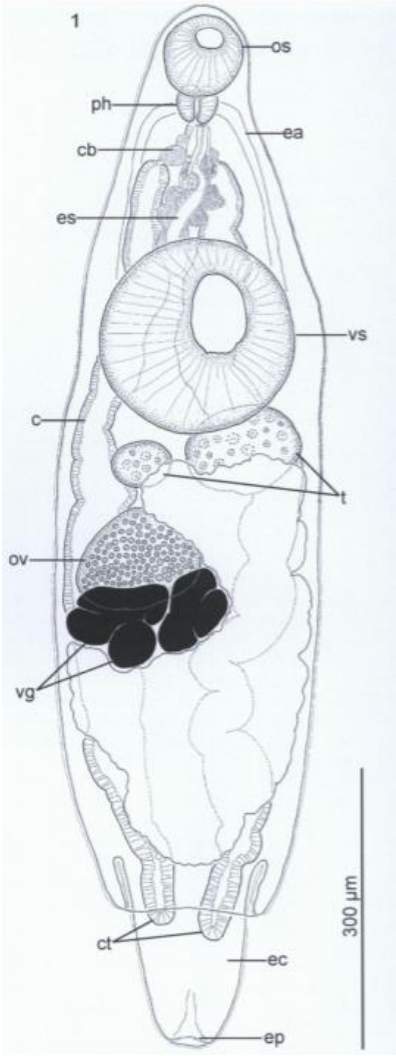
Lecithochirium floridense (Manter, 1934) Crowcroft, 1946

Description: Body elongate. Tegument plicated with papillae. Escoma present, either extended or withdrawn. Oral and ventral sucker present. Size ratio 1:2.5. Pharnyx present. Located directly posterior to oral sucker. Genital pore median directly posterior to gut bifurcation. Two testes present, dissimilar in size, subspherical, opposite, located at posterior margin of ventral sucker. Ovary dextral, subspherical, located posterior of testes in middle third of hind body. Vitellaria contained in two lobed masses. Vitellaria contained to middle third of hind body overlapping the ventral margin of the ovary. Uterus extensive, extending anteriorly and posteriorly of ovary, sometimes extending into escoma. Eggs numerous, oblong in shape.

Host: *M. curema*

Location: Gills

Taxonomic/Image Reference: Bullard et al 2011. Page 834. Figure 1.



Lecithochirium monticelli (Linton, 1898) Crowcroft, 1946

Description: Body elongate. Tegument smooth with papillae present. Escoma present. Oral and ventral suckers present. Size ratio 1:5. Genital pore median directly posterior to oral sucker at level of pharynx. Testes present, dissimilar in size, opposite. Testes located at the ventral margin of the ventral sucker. Ovary located in the hind body. Vitellaria contained in two long lobed masses directly posterior to ovary. Eggs large. Contained in extensive ovary that extends anteriorly and posteriorly of ovary.

Host: *M. curema*

Location: Gills

Taxonomic Reference: Bullard et al. 2011

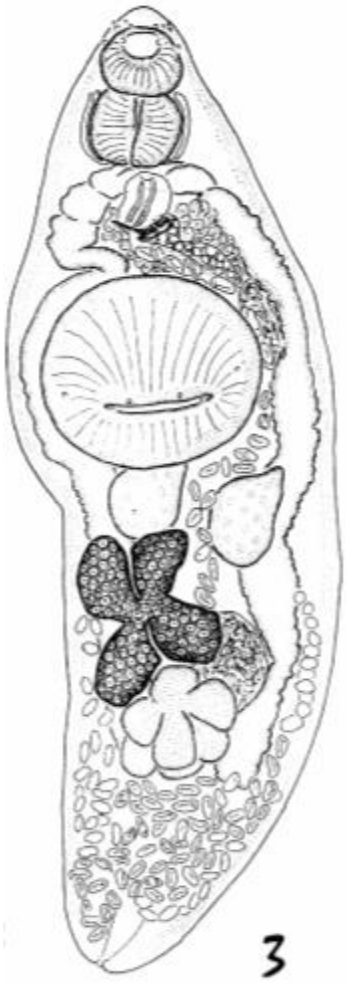
Lecithaster helodes Overstreet, 1973

Description: Elongate body. Tegument no spinous. Four pairs of papillae near mouth. Oral and ventral sucker present, size ratio 1:2.5. Pharynx wide and larger than oral sucker. Genital pore median at level of gut bifurcation. Testes ovoid, opposite, and located anterior of ovary. Vitellaria contained to mid-hind body in seven spiral lobes. Eggs contained to the mid-hind body extending to posteriorly to end of body

Host: *M. curema*

Location: Intestines

Taxonomic/Image Reference: (Overstreet 1973) Page 236. Figure 3.



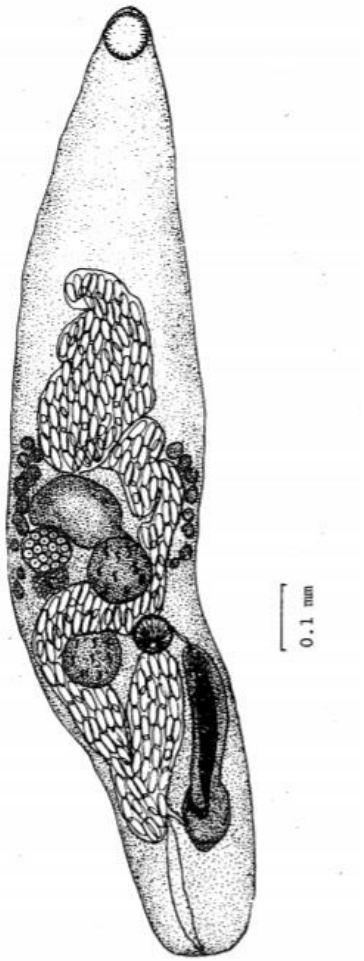
Prosorhynchoides longoviferus (Manter, 1940)

Description: Minuscule elongate worm. Simple oral sucker, ventral sucker absent. Vitellaria contained to mid body at level of mouth and in form of 8-10 oval masses on both the dextral and sinstral side of body. Eggs long and slender and contained throughout mid and sometimes hind body; more distinctly extending anteriorly of vitellaria. Mouth located in mid body at same level as ovary. Testes postovarian and opposite. Cirrus sac present in hind body and extending anteriorly to level of testes.

Host: *S. barracuda*

Location: Intestines

Taxonomic/Image Reference: Corkum 1963. Page 184, Plate VIII



Rhipidocotyle longleyi Manter, 1934

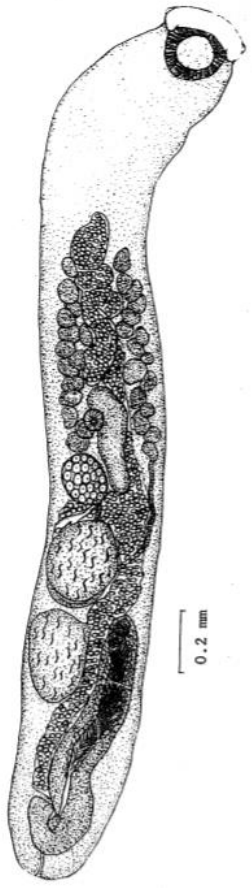
Description: Body elongate. Tegument smooth. Complex oral sucker with five anterior lobes. Ventral sucker absent. Vitellaria contained to the mid body in the form of 10-15 oval masses that are located along the sinstral and dextral body margins. Mouth located at the midline of vitellaria. Ovary subspherical at overlapping with posterior margin of mouth. Testes subsperical and located postovarian and tandem to one another. Uterus contained to hind body. Eggs numerous. Cirrus sac present in the hind body and extending anteriorly to the level of the testes.

Host: *S. barracuda*

Location: Intestines

Taxonomic References: Ward 1954

Image Reference: Corkum 1963 Page 206. Plate XIX



Rhipidocotyle longicirrus (Nagaty, 1937) Baartoli & Bray, 2005

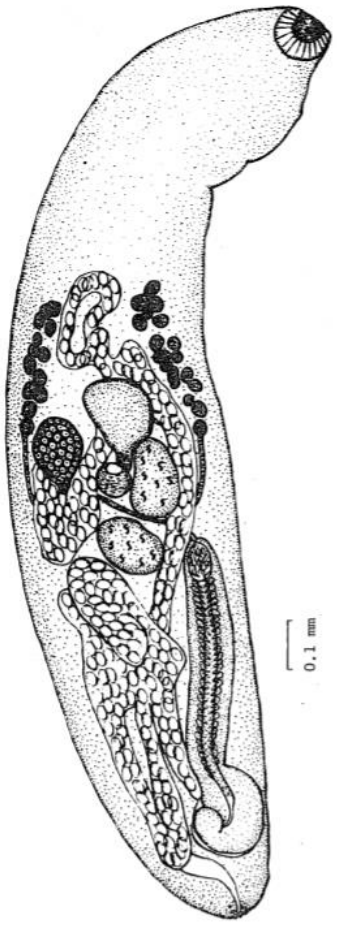
Description: Body elongate, linguiliform. Body markedly narrowly at level of vitellaria and widest directly posterior to vitellaria. Tegument heavily spinous. Simple oral sucker present with lobed rynchus. Ventral sucker absent. Vitellaria in eight to ten lobed masses on both sinstral and dextral margins of body. Vitellaria masses containing overlapping anterior and posterior margins. Ovary dextral, subspherical, located at the posterior margin of vitellaria. Testes subspherical, dissimilar in size, tandem, post-ovarian. Mouth location varies, usually extending posteriorly in between the level of the ovary and anterior most teste. Mouth can extend to the most posterior margin of the most anterior teste. Uterus winds throughout the midbody and hindbody. Cirrus sac present in terminal hind body extending anteriorly to the level of testes.

Host: *S. barracuda*

Location: Stomach & Intestines

Taxonomic Reference: Bartoli & Bray 2005

Image Reference: Corkum 1963. Page 182, Plate VII.



Saturnius belizensis Fischtal, 1977

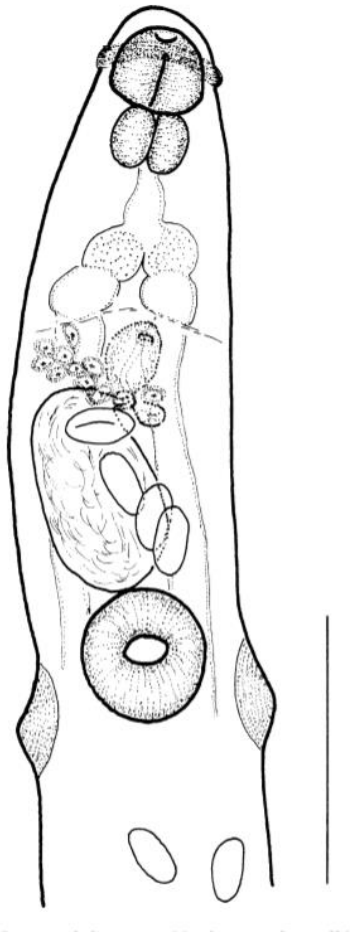
Description: Body small, elongate. (BL:415-594ɯm; BW:65ɯm) Oral and ventral suckers present. Both small in size. Size ratio 1:1.38. Pharnyx well developed. Body divided with three septa into four distinct pseudosegments. Blasco et al. (2006) stated that there were only three septa present in this species but Blasco et al (2008) found that an additional faint septa located at the level of the genital pore. This additional septa was not seen in described specimens from this study. Three circular muscular flanges present. The first creates a well-developed muscular halo at the level of the oral sucker. The second flange strongly developed, overlapping with the posterior margin of ventral sucker. The third septa located in the posterior third of last pseudosegment, weak development. Testes two, subspherical, tandem, located in the second and third pseudosegment. Ovary ovoid, in fourth pseudosegment. Genital pore median, inbetween oral and ventral sucker. Seminal vesicle elongate-saccular. Eggs numerous and large

Host: *M. curema*

Location: Stomach

Taxonomic Reference: Blasco-Costa et al. 2006

Taxonomic/Image Reference: Blasco-Costa et al. 2008. Page 66, Figure 9.



Saturnius maurepas Overstreet, 1977

Description: Body small, elongate. (BL: 720ɯm; BW: 82ɯ). Body separated into 7 pseudosegments separated by 6 septa. Two septa located in the anterior half of body. One at level of genital pore, one directly anterior to ventral sucker, thick. Three muscular flanges present. First flange at midlevel of oral sucker. Second flange at level of ventral sucker weakly developed, mound shaped. Third flange located in the posterior region of the most posterior pseudosegment. Seminal vesicle large, wide-tubular. Testes two, subspherical, tandem. Ovary ovoid, in posterior most pseudosegment. Vitellaria ovoid, sub-triangular, large, occupying most of posterior most segment.

Host: *M. curema*

Location: Stomach

Taxonomic Reference: Blasco-Costa et al. 2008

Scaphanocephalus expansus (Creplin, 1842)

Description: Encysted metacercariae. Body elongate, Wing like projections on anterior end. Tegument scaly. Oral sucker present, small, located anteriorly. Prepharynx short. Pharynx small. Gut bifurcated, ending blind. Genital pore median, uterus long and spiral lobed. Vitellaria confined to dextral and Sinstral sides of body extending anteriorly to the level of caecum. Samples from *M. curema* found as encysted metacercariae showing that *M. curema* is one of the intermediate host for this species.

Host: *M. curema*

Location: Fins

Taxonomic/Image Reference: Bray et al. 2008. Page, Figure 5.24.

Schikhobalotrema elongatum Nahhas & Cable, 1964

Description: Body elongate. Oral and ventral sucker present, similar in size. Oral sucker sub-triangular at anterior end of the body. Ventral sucker sub-circular located in second fourth of body. Pharynx well developed. Prepharynx short. Gential pore sharing posterior margin with pharynx, median. Prostate cells ducts forming bulbous masses directly posterior to genital atrium.Testes two, elongated, median, opposite, in posterior half of body. Ovary ovoid, pre-testicular, posterior of ventral sucker. Eggs large, numerous. Vitellaria follicular extending anteriorly of ventral sucker to posterior end of body.

Host: *M. curema*

Location: Intestines

Taxonomic/Image Reference: Nahhas & Cable 1964 Pages 182 & 185, Figure 12

Stephanostomum ditrematis (Yamaguti, 1939) Manter, 1947

Description: Body elongate. Oral sucker ovoid 15-20 spines present on the most anterior end. Pharnyx well developed and located at level of gut bifurcation. Ventral secuker located in the anterior most quarter of the body. Similar in size to the oral sucker. Vitellaria follicular and contained to the posterior half of body. Genital pore directly anterior of ventral sucker. Uterus spiral and located in the second quarter of the body. Eggs small, numerous throughout uterus. Ovary circular and pretesticular. Testes tandem and ovoid.

Host: *C. hippos*

Location: Intestines

Taxonomic/Image Reference: Sogandares-Bernal & Hutton 1959

Nematoda

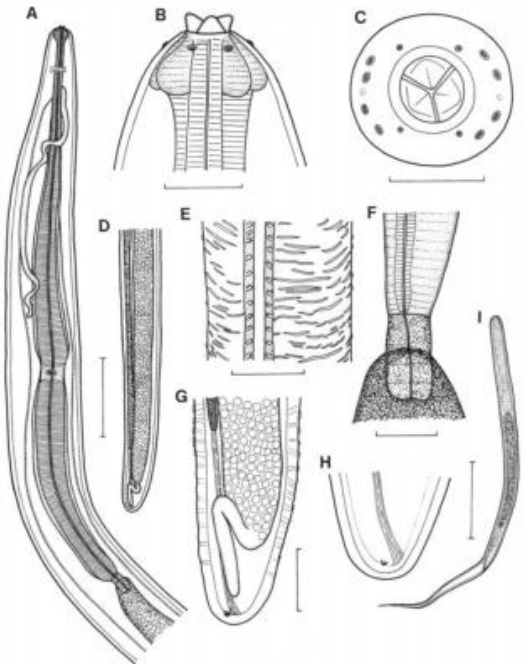
Caranginema americanum

Description: Posterior end of body distinctly narrowed. Cephalic end truncated Cuticle thick. Two elevated cordons extending on each side of the body starting at the level of the esophagus and extending into the caudal end of the worm. Oral aperature circular surrounded by a thick ring of smooth cuticle. Eight papillae in outer circle arranged in four submedian pairs and four submedian pairs of papillae in inner circle. Three large sclerotized conical teeth protruding out of the mouth. Esophagus forming distinct subcircular bulb.

Host: *C. hippos*

Location: Subcutaneous around dorsal and anal fins

Taxonomic/Image Reference: Moravec et al. 2008



Contracecum sp. larvae

Description: Encysted stage second and third stage larval nematode. Body extended and elongate. Cuticle thick. Anterior end truncated. Posterior end tapers to point. One boring conical tooth extending out of mouth. Folded circular collar present as distal margin of cephalic region. Esophagus not completely developed in stage two larvae. Two cordons present in body. The first located in the anterior half of body and the other in the posterior half. Intestinal cecum present

Host: *C. hippos*, *S. barracuda*, *M. curema*, *G. cinereus*, and *S. marina*

Location: Intestines, and Phylloric Cecae

Taxonomic Reference: Gibbons 2010

Cucullanus sp. larval

Description: Encysted stage third stage larval nematode. Body extended and elongate. Cuticle thin. Cephalic region bulbous. Posterior region tapers to abrupt point. Three lips present in mouth. Two pairs of papillae present in cephalic region. Mouth opening perpendicular to body axis. Cuticularized pieces frame mouth opening. Intestinal caecum absent.

Location: Intestines, and Phylloric Cecae

Host: *C. hippos*

Taxonomic Reference: Arai & Smith 2016

Copepoda

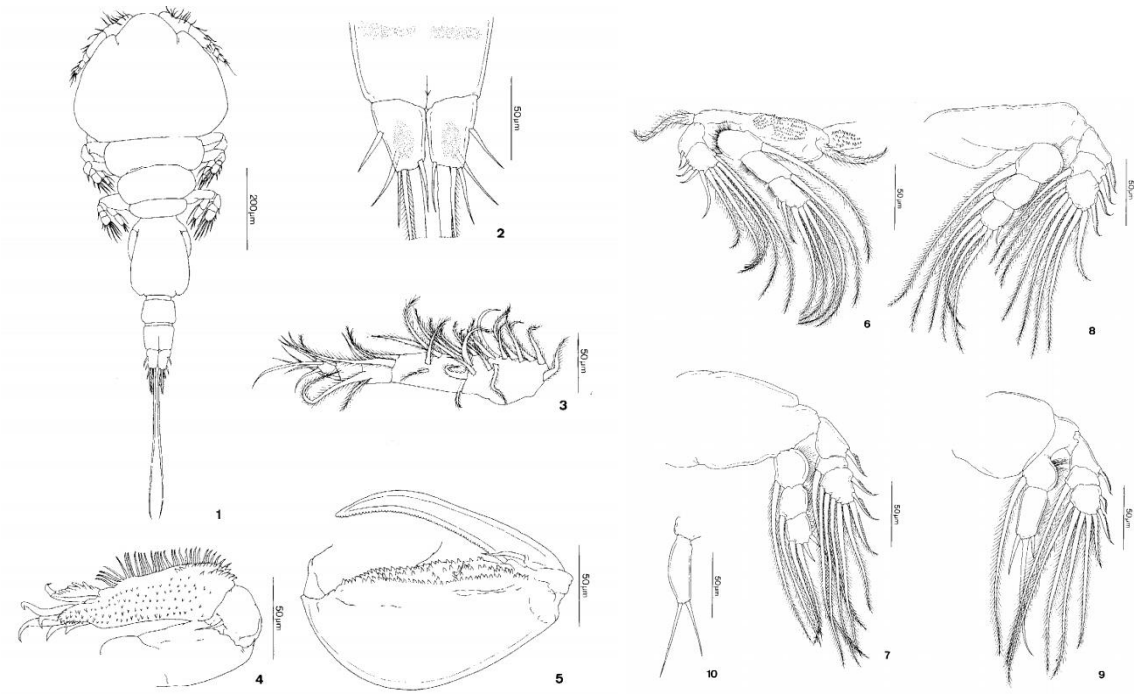
Bomolochus nitidus Wilson C.B. 1911

Description: Genital complex well developed. Abdominal segment composed of two segments. Two uropods present with six setae located at the end of each. Entire ventral surface covered with spinules. First antennae with five segments, and second antennae with three segments. The basal segment is unarmed. Maxilliped three segmented with robust medial segment armed with vertical rows of denticles and one seta. Distal segment modified into a claw. First leg sympod armed with spinules and two long pinnate setae. Second, third, fourth, and fifth legs unarmed. Second and third leg with three segmented rami. Fourth and fifth legs with two-segmented rami.

Host: *M. curema*

Location: Gill Filaments

Taxonomic/Image Reference: Knoff et al. 1994, Page 47-48, Figure 1-10



Ergasilus lizae von Nordmann, 1832

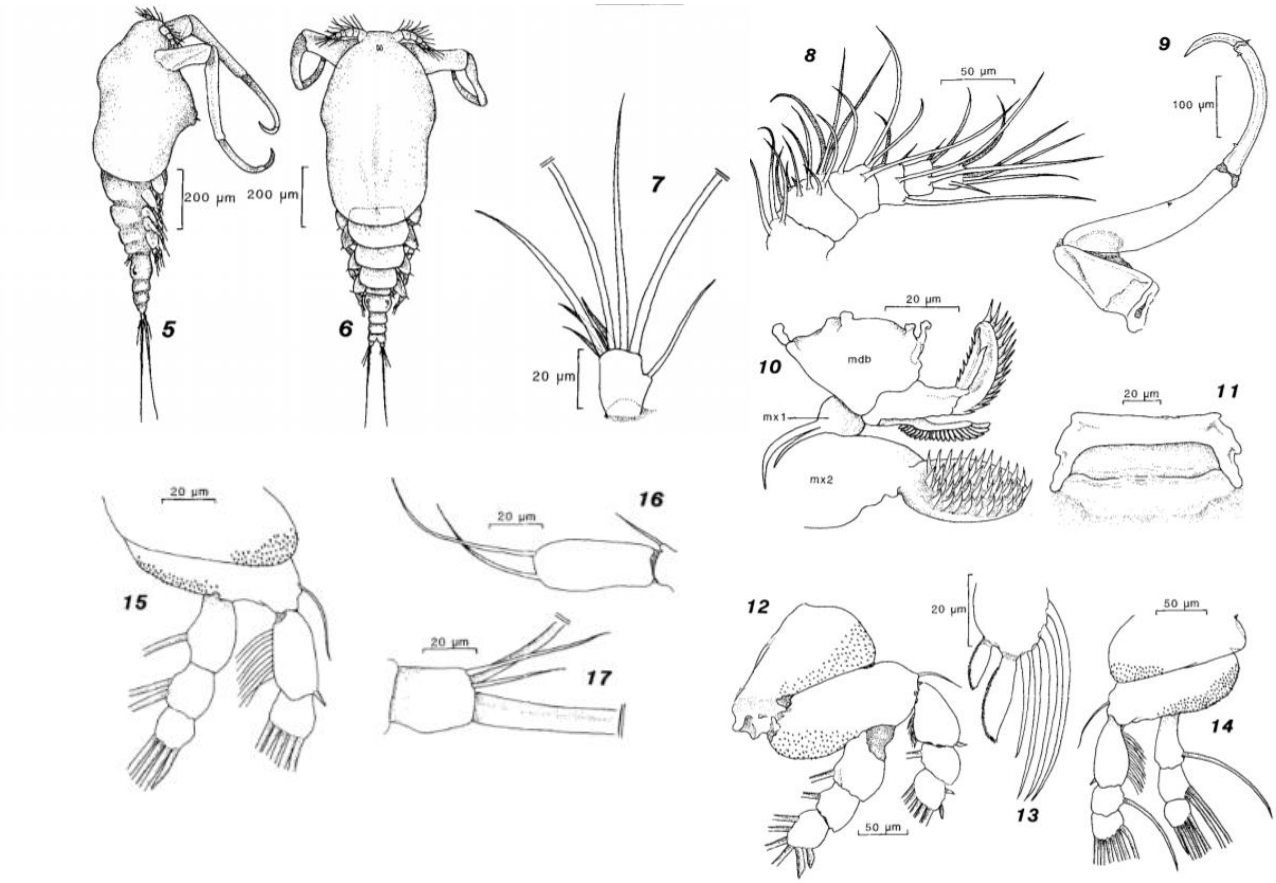
Description: Cephalothorax oblong, slightly narrower at the midline of cephalothorax, violin shaped. Second to fourth pedigerous segments gradually reducing in width. Fifth pedigerous very short and narrow. Genital complex subspherical and located after fifth pedigerous. Abdomen made up of three segments, dissimilar in size, third segment with deep posterior notch. First antenna six segmented, apical armature with four long and three short setae. Second antenna subchelate, well developed, narrow, with curved end ending in unarmed claw. First four pairs of legs biramous, fifth leg uniramous, fourth expod two segmented, all others three segmented. Spines at tip of first endopod. Fifth leg two segmented. Caudal ramus long, narrow, with one long and thick unarmed setae, one shorter and slender setae and two significantly shorter setae.

Host: *M. curema*

Location: Gill Filaments

Taxonomic Reference: Kabata 1988, Page 98-100; Kabata 1992, Page 48-52.

Image Reference: Kabata 1992, Page 4952, Figures 5-17.



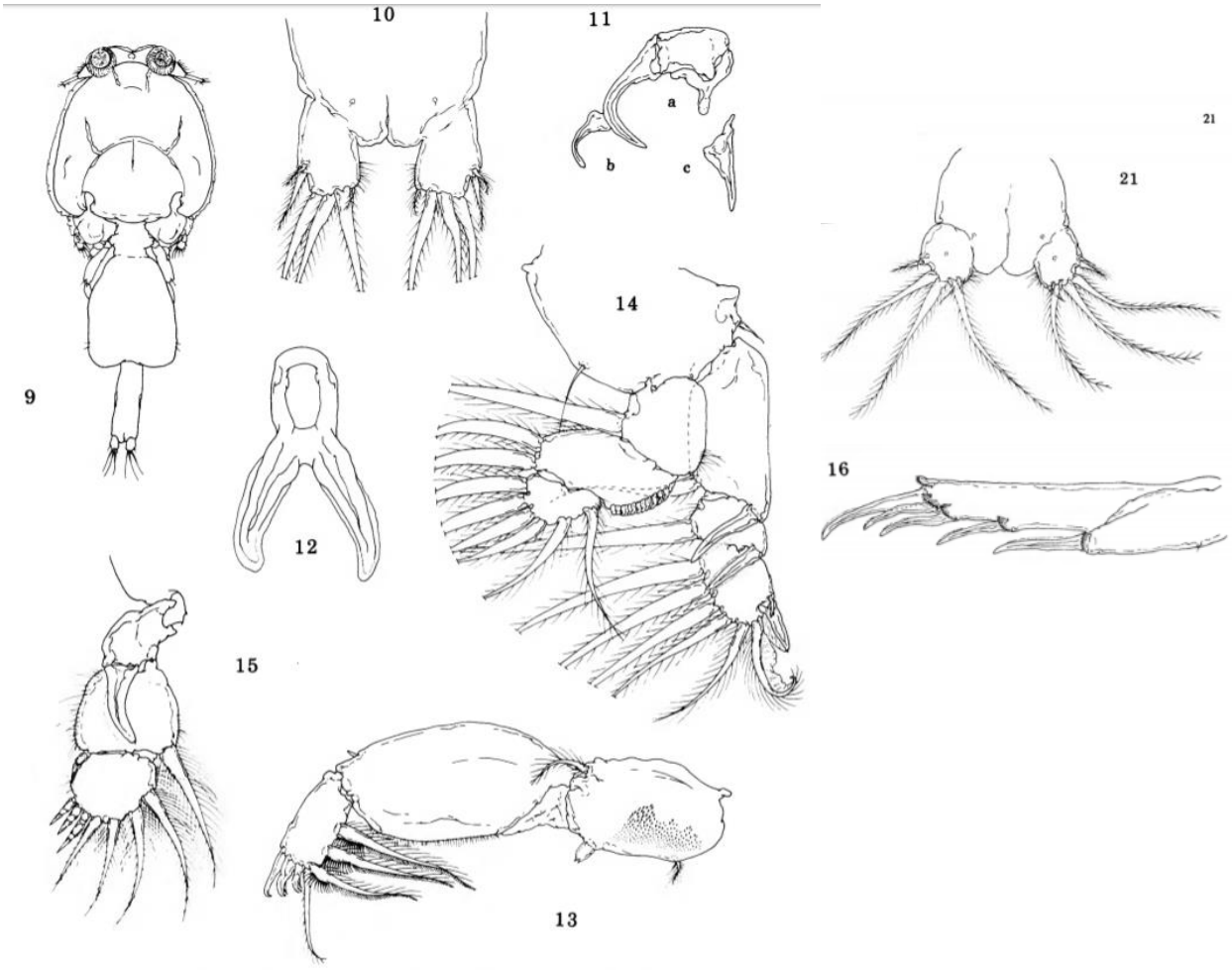
Caligus asperimanus Pearse, 1951

Description: Cephalothorax longer than wide, consisting of less than half of the total body length, dorsoventrally flattened. Genital complex longer than wide, widest posteriorly ending in shallow dip, consisting on one third of body length. Abdomen connected posteriorly to genital complex, three times as long as wide, posterior end with deep notch. Caudal ramus with three long, wide unarmed setae, one short, narrow setae, two significantly smaller setae. Lunules moderately separated, similar in width to the distance between the lunules. Second antennae with recurved distal hook with posterior spine. Cephalothorax containing first three leg bearing segments and fourth leg segment small. Spiniform process on first leg with three terminal spines. Exopod of leg two with spinous process. Exopod of leg 4 with two segments, first segment with long spine, second segment four long spines.

Host: *S. marina*

Location: Gill Filaments

Taxonomic/Image Reference: Cressey 1991. Pages 2-3, 20-21, Figures 9-15.



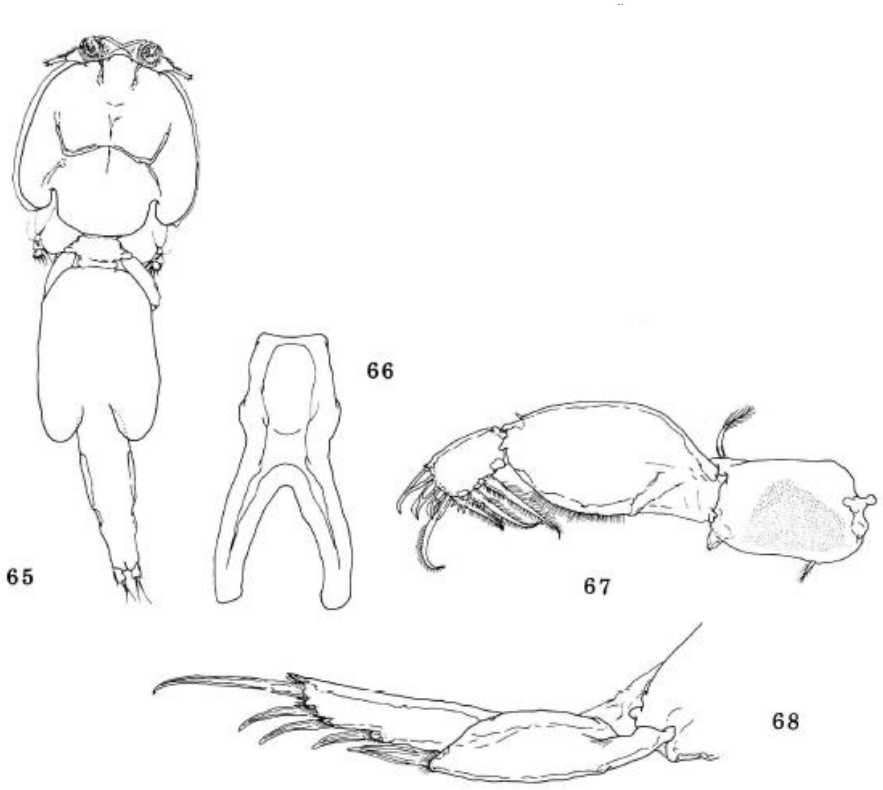
Caligus bonito Wilson C.B., 1905

Description: Cephalothorax almost as long was wide. Genital complex two times longer than wide. Abdomen four times longer than wide, ventral surface with patch of spinules on each posterior corner. All three body sections similar in length. Lunules moderately separated. Width of lunule slightly narrower than the distance between lunules. Second antennae bearing large recurved claw. First three leg bearing segments on cephalothorax. First leg exopod three segmented, medial lateral setae with rows are stout spines on basal outer margin.. Fourth leg two segmented with one short, thick spine on first segment, and three short narrow spines as well as one long, narrow spine on second segment.

Host: *M. curema*

Location: Gills

Taxonomic/Image Reference: Cressey 1991. Page 5-6, 28, Figures 65-68.



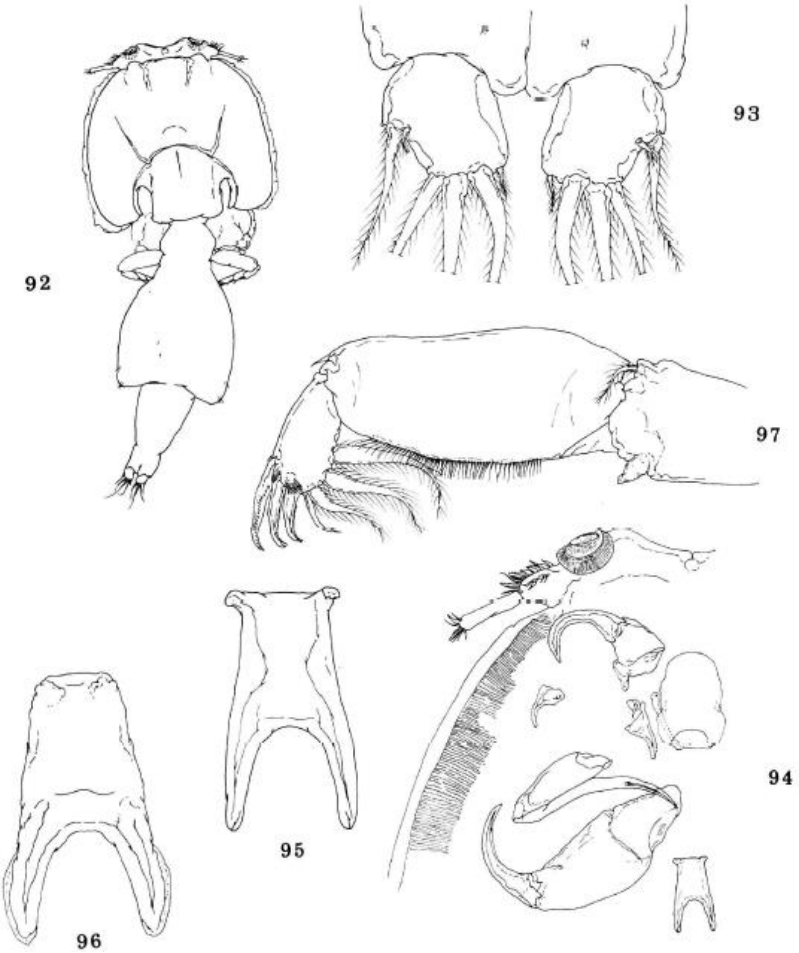
Caligus isonyx Steenstrup & Lutken, 1861

Description: Cephalothorax slightly more wide than long, accounting for about one third of body length. Genital complex sub-triangular, widest posteriorly. Free fourth pedigerous somite and genital complex about as long as cephalothorax. Abdomen consists on final third of body. Widest anterior narrowing at the last third of abdomen. First three legs segment contained in the cephalothorax. Lunules widely spaced. Second antennae ending in claw bent at 90 degree angle. Exopod of leg bearing small spines at outer distal corner and three terminal spines. Exopod of leg two, first segment, with prominent serrated spine at outer distal corner. Second segment with similar smaller spine. Segment on of leg three with thick, large recurved spine. Leg four with three segments, segments on and two with one long, thick spine, third segment with three narrower, long spines that gradually get longer.

Host: *S. barracuda*

Location: Gills

Taxonomic/Image Reference: Cressey 1991, Page 8-9, 32-34, Figures 92-97



Caligus lobodes (Wilson C.B., 1911)

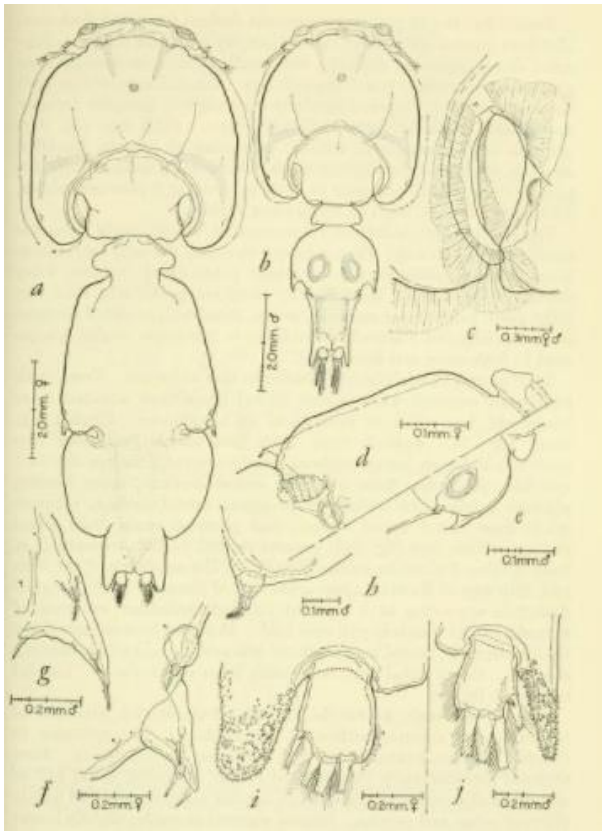
Description: Body elongated, strongly flattened. Red to brown in color. Cephalothorax elliptical, accounting for 3/5 of body length in female. Accounts for more than half of body length for males. Lunules small, widely separated. Free segment half of the width of genital complex, widen posteriorly at attachment of fourth pair of biramous legs. Genital complex and abdomen varies based on sex. Female: Genital complex in the shape of inverted U, squared posteriorly, 2/3 of the length of cephalothorax. Abdomen similar in length to genital complex. Two-jointed with large semi-elliptical lobes on either margins of the basal joint. Lobes are as long as the segment that they are attached to. Posterior segment of abdomen shaped into cylindrical lobe ending squarely truncated, spines on terminal end of lobes sinstrally and dextrally. Male: Genital complex oovoid in shape, accounting for a quarter of body length. Spines located at either side of terminal end of genital complex. Abdomen similar in size to genital complex, cylindrical in shape ending squarely. Individuals of this species were found around eyes and on the external portion of the operculum.

Host: *S. barracuda*

Location: External

Taxonomic Reference: Wilson 1911, identified as synonymized name *Midias lobodes.*

Image Reference: Lewis 1967, Page 95, Figures a-j. a: female, b: male



Caligus productus Dana. 1852

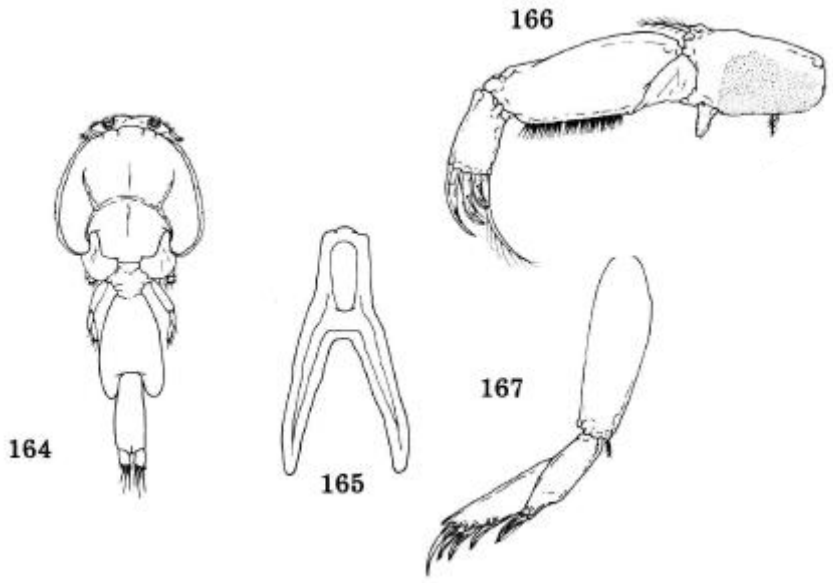
Description: Body elongate, flattened. Cephalothorax ovoid. Lunules small, moderately separated. Genial complex and abdomen together are similar in size to cephalothorax. Genital complex and abdomen sexually dimorphic. Female genital complex ending in postero-lateral lobes. Abdomen two-segmented, first segment slightly shorter than second. Male genital comples sub-triangular with small spines on terminal lateral sides. Abdomen two-segmented, second segment twice as long as first. Post-antennal process longer and more curved in males. Lacking three median lateral setae on first leg. Leg four three segmented. Second second with one spine and third segment with four spines, increasing in length towards the terminal spine.

Host: S. *barracuda*

Location: Mouth

Taxonomic Reference: Boxshall & El-Rashidy 2009

Image Reference: Cressey 1991, Page 43, Figure 164-172



Caligus spinosus Yamaguti, 1939

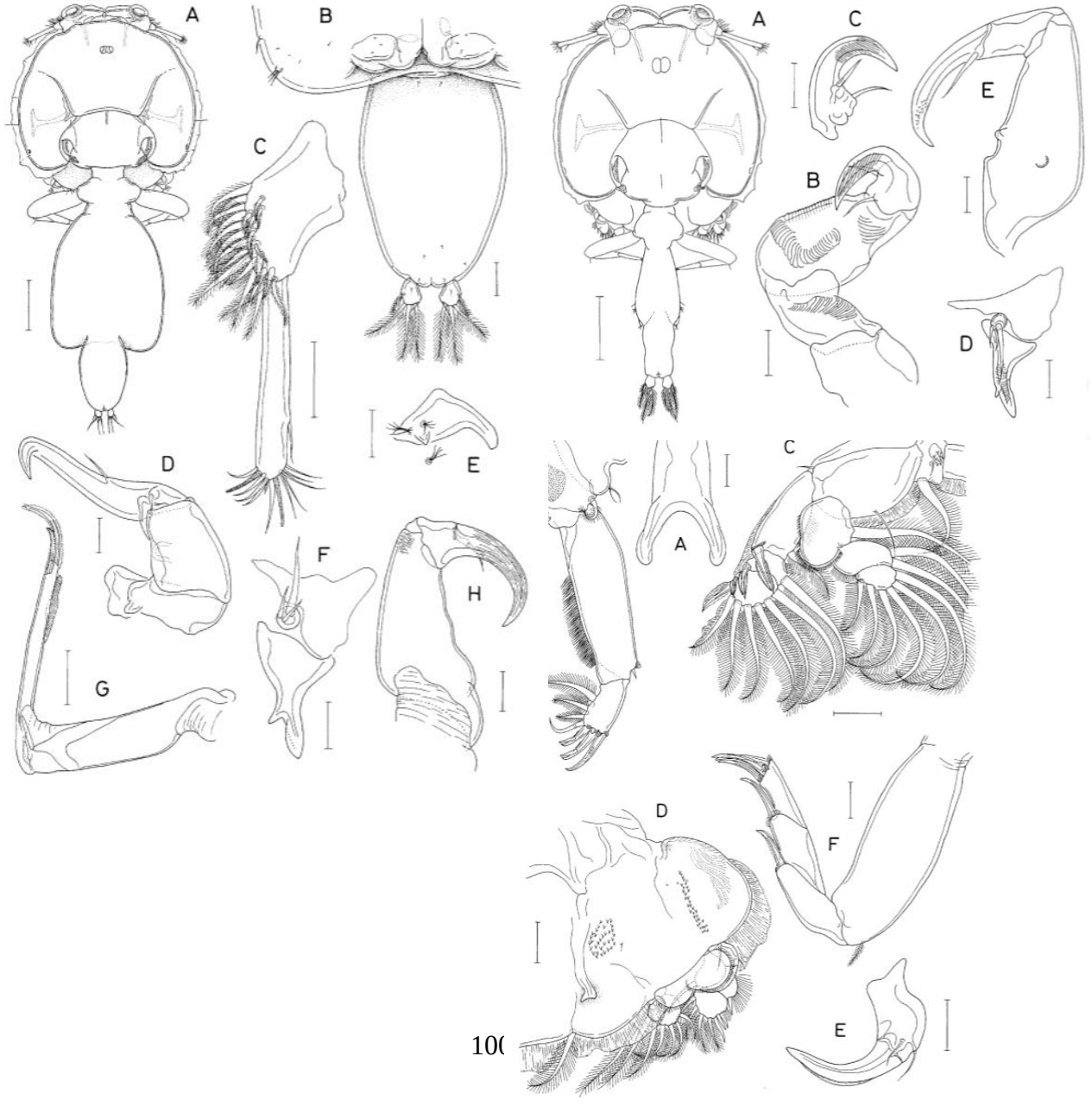
Description: Body elongate, flattened dorsal ventrally. Cephalothorax subcircular. Lunules moderate in size, close together. Fourth pedigerous segment fused to genital complex. Female genital complex gradually broadening distally truncating squarely, similar in size to cephalothorax. Abdomen half the size of genital complex broadly rounded. Male genital complex completely fused to abdomen forming elongate genito-abdomen. Antennule two-segmented with 25 pinnate seta, distal segment elongated with 11 naked setae.

Host: *C. hippos*

Location: Gills

Image/Taxonomic Reference: Chloe & Kim 2010, Page 25-27, Figures 1-3.

Top Left – Female, Top Right – Male



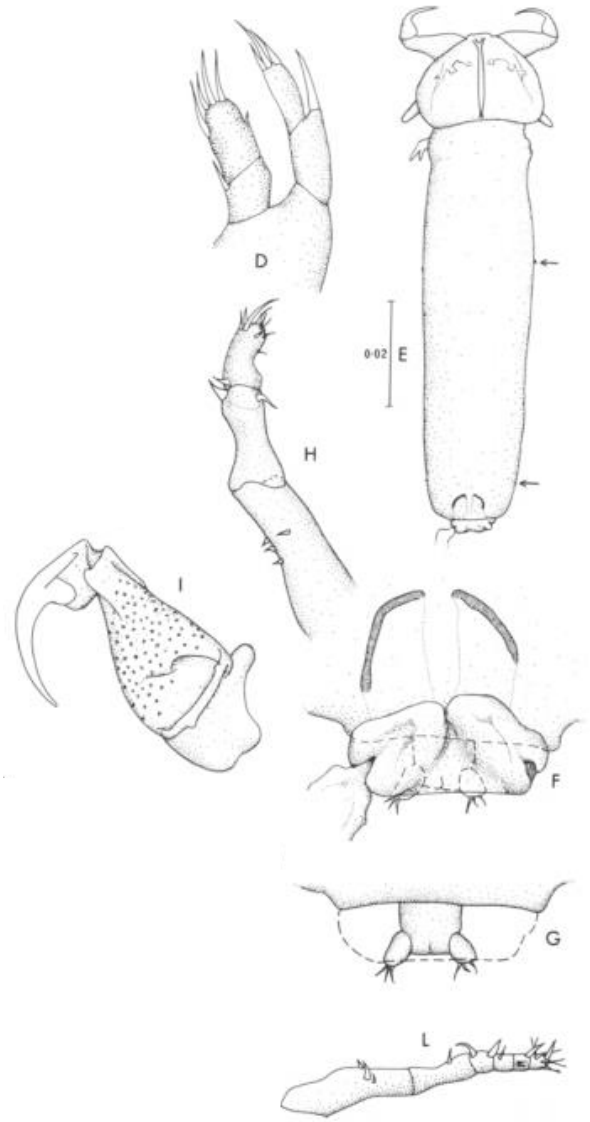
Hatschekia amplicapa Pearse, 1951

Description: Body elongate. Cephalathorax wider than long, heart-shaped. Trunk cylindrical. Posterior margin truncated. Abdomen wider than long with two uropods with three setae. First set of antennae three-segmented. Second pair of antennae distinct ending in claw with swollen base. Leg one, two-segmented with last segment bearing three short spines. Leg two, two segmented. First segment with terminal spine. Second segment also bearing spines.

Host: *S. marina*

Location: Gill Filaments

Taxonomic/Image Reference: Jones 1902, Page 227, Figures E-J.



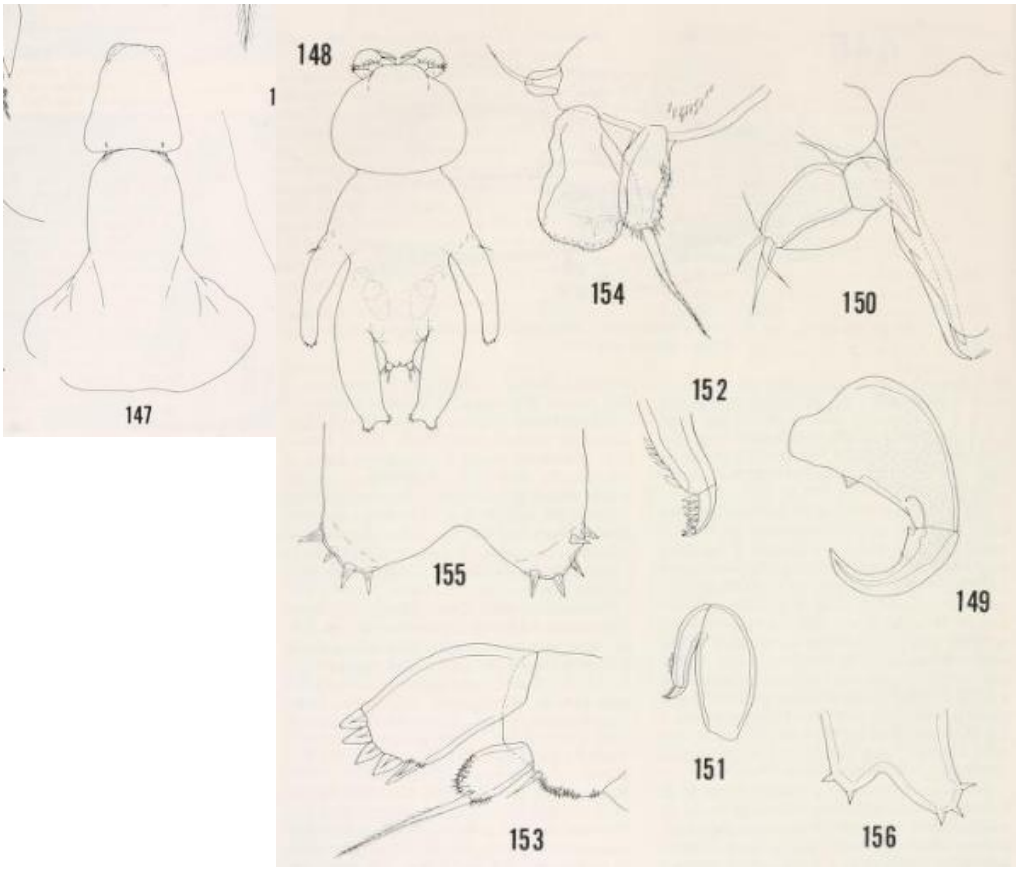
Lernanthropus belones Krøyer, 1863

Description: Female: Cephalothorax rectangular, more wide than long, accounting for one third of body length. Horns on either side of ceohalothorax at the most anterior end. Dorsal shield shaped with cape like structure, accounting for two thirds of body length. Male: Cephalothorax ovoid accounting for one quarter of body length. Abdomen pyriform, accounting for one half of body length. Second antennae ending terminally in a simple claw with surface covered in small spines. First leg one segmented with five broad spines. Second leg one segmented with distal border bearing rows of spincules. Third leg modified into elongate lateral process bearing multiple short spines. Fourth leg in form of elongate process with bifurcated tip.

Host: *S. marina*

Location: Gills

Taxonomic/Image Reference: Cressey & Collette 1970, Page 383, Figure 147/ Page 388, Figure 148-156



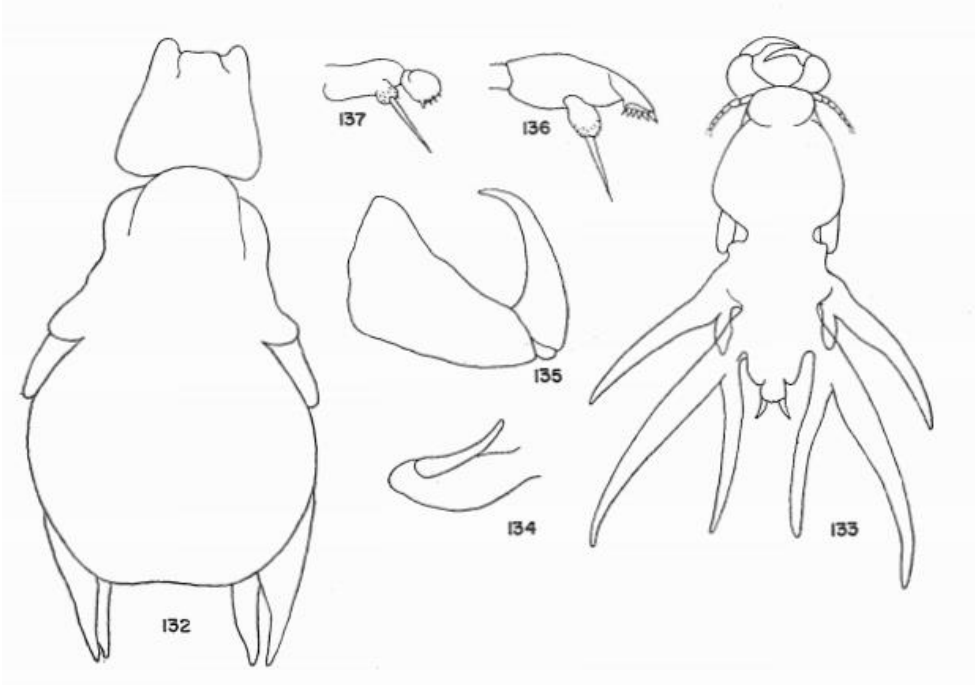
Lernanthropus giganteus Krøyer, 1863

Description: Female: Cephalothorax slightly longer than wide, trapezoidal in shape. Horn-like antennae protruding from anterior margin of cephalothorax. Dorsal plate narrox anteriorly and bulbous posteriorly. Third pair of legs folded and projecting ventrally at right angles. Fourth leg dived at the base with broad flattened bases and pointed tips. Male: Cephalothorax longer than wide, trapezoidal in shape. Cephalothorax separated from the rest of the body by neck like structure. No dorsal plate present. Genital segment rounded and short. Abdomen short with a pair of tapering caudal rami. First and second pair of legs with long spine present on endopodite and short spine on exopodite. Thirds and fourth legs biramus, divided at the base. In third leg endopod is very short.

Host: *C. hippos*

Location: Gill Filaments

Taxonomic/Image Reference:



Isopoda

Rocinela signata Schioedte & Meinrt, 1879

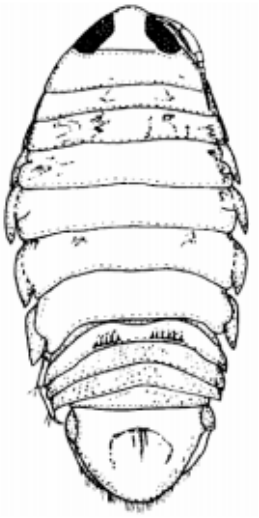
Description: Body fusiform, dorsal ventrally flattened. The first three sets of legs end distally in large hooks. Cephalon tapered to rounded dorsal end with two large continuous eyes. Seven pereonites present and four pleonites. Maxilliped palp two-segmented. The last four pairs of legs lack hooks and end terminally in straight segments. Pleotelson adorned with M or W shaped mark.

Host: *S. barracuda*

Location: Gills

Taxonomic Reference: Rafi 1988

Image Reference: Bunkley & Bunkley Williams 1996



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Appendix 3: Host Fish Size Class Determination Graphs

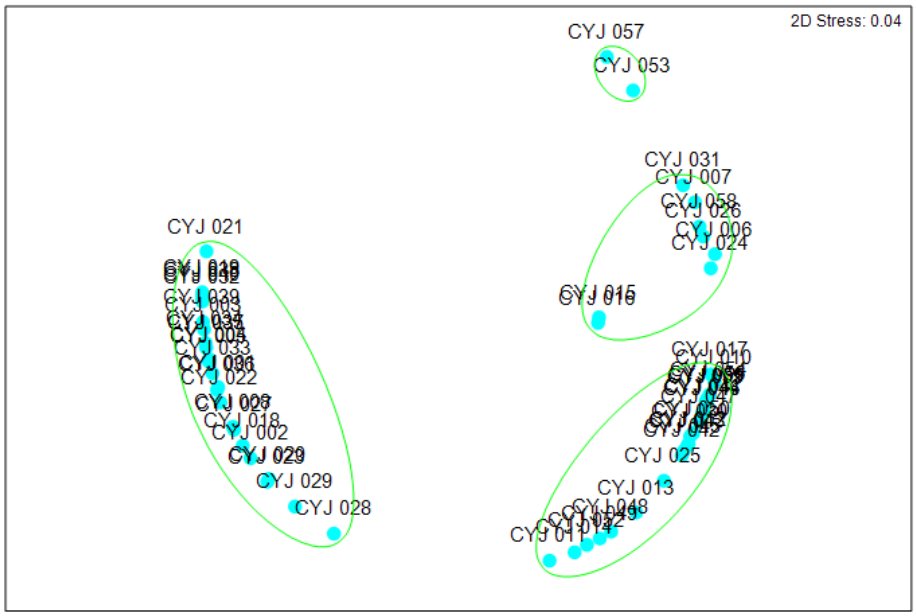

Figure 1a. Non-metric MDS of length and weight measurements of all sampled *C. hippos* individuals transformed by Log(X+1) and resembled by Euclidean distance used to determine the four size classes. Distance between clusters is 1.

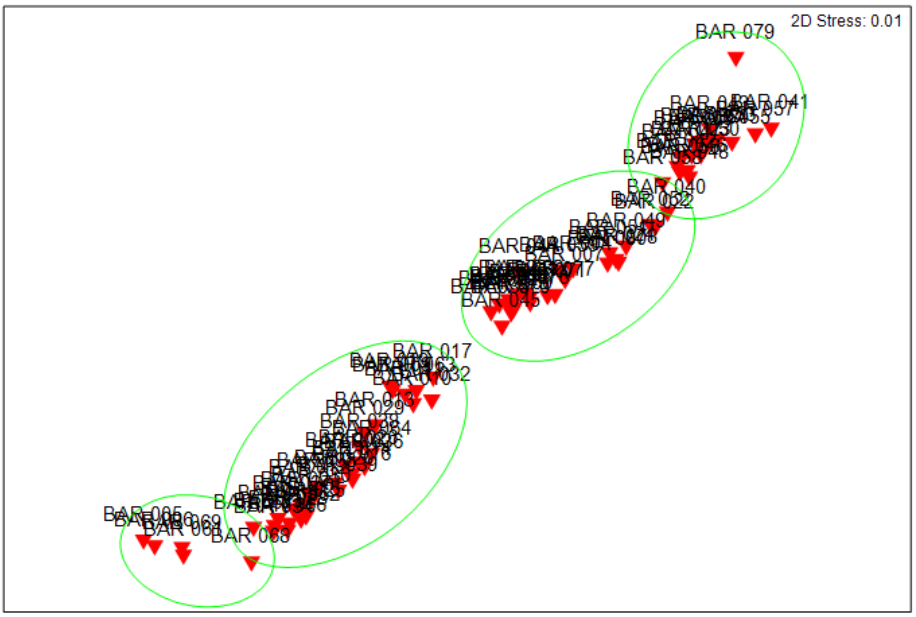

Figure 2a. Non-metric MDS of length and weight measurements of all sampled *S. barracuda* individuals transformed by Log(X+1) and resembled by Euclidean distance used to determine the four size classes. Distance between clusters is 1.7.

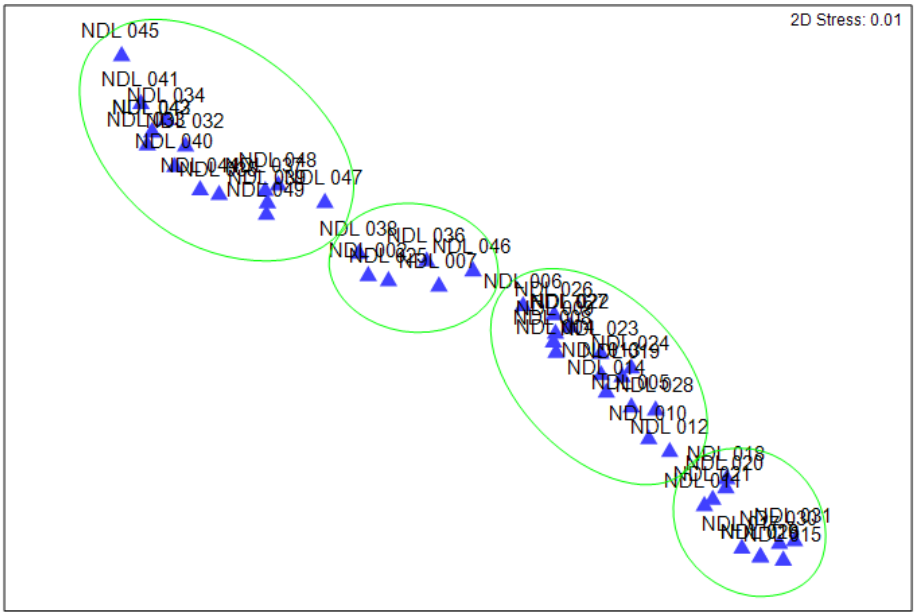

Figure 3a. Non-metric MDS of length and weight measurements of all sampled *S. marina* individuals transformed by Log(X+1) and resembled by Euclidean distance used to determine the four size classes. Distance between clusters is 1.5.

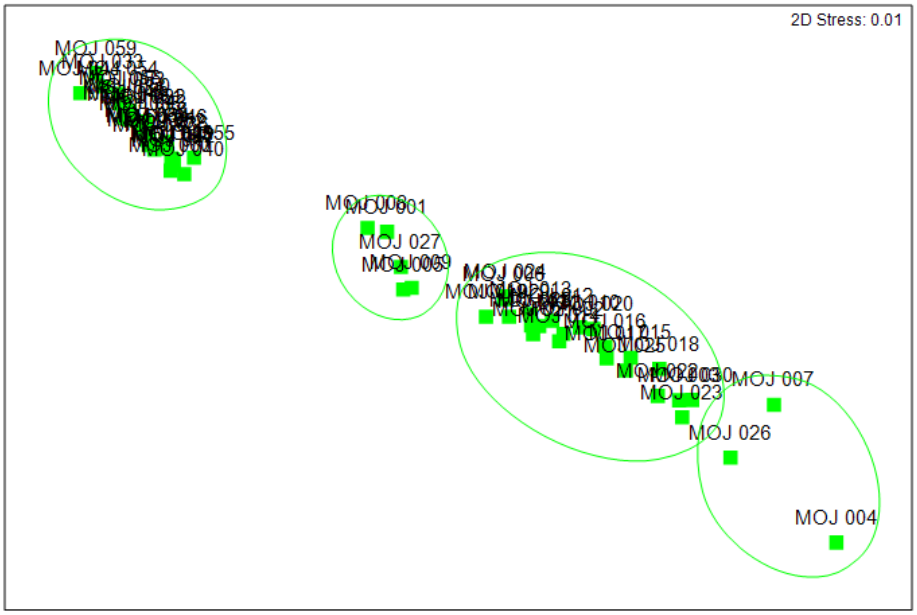

Figure 4a. Non-metric MDS of length and weight measurements of all sampled *G. cinereus* individuals transformed by Log(X+1) and resembled by Euclidean distance used to determine the four size classes. Distance between clusters is 1.3.

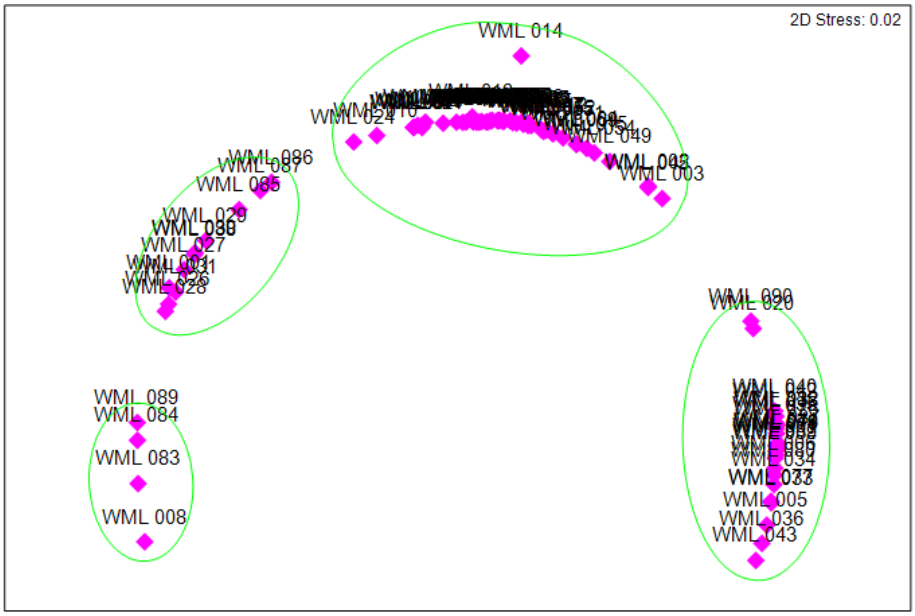

Figure 5a. Non-metric MDS of length and weight measurements of all sampled *M. curema* individuals transformed by Log(X+1) and resembled by Euclidean distance used to determine the four size classes. Distance between clusters is 0.98.